The American Midland Naturalist

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CONTENTS

Studies on Virgin Hardwood Forest: II, a Comparison of Quadrat Sizes in a Quantitave Phytosociological Study of Nash's Woods, Posey County, Indiana—*Stanley C. Cain* 529

A Notable Case of Bog Formation—*J. E. Potzger* 567

Prof. Shepard's Trees of Greene County—*Benjamin Franklin Bush* 581

Studies on Cestoda of Poultry Found in and around Douglas County, Kansas—*Q. B. Ferry* 586

The Distribution of the Downy Woodpecker (Dryobates pubescens) in Eastern Kansas—*W. S. Long* 598

Epistominoides and Coleites, New Genera of Foraminifera—*Helen Jeanne Plummer* 601

A New Species of Dicranopeltis—*Carol Y. Mason* 609

Some Atlantic Coast Tertiary Pectinidae—*H. I. Tucker* 612

Hypertrophy in the Jaw of an Oklahoma Proboscidean—*J. Willis Stovall* and *C. Stuart Johnston* 622

Book Reviews 625

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The American Midland Naturalist

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STUDIES ON VIRGIN HARDWOOD FOREST: II,

A COMPARISON OF QUADRAT SIZES IN A QUANTITATIVE PHYTOSOCIOLOGICAL STUDY OF NASH'S WOODS, POSEY COUNTY, INDIANA

STANLEY A. CAIN

The use of scattered sample plots, or quadrats, seems to have been introduced by Pound and Clements (1898) and associates in so far as American ecology is concerned, but the amplification of their use and the critical study of plant communities by means of them has been developed largely by European phytosociologists. A recent translation by Fuller and Conard (1932) of a leading text in the field, namely Braun-Blanquet's "Pflanzensoziologie," will undoubtedly stimulate such investigations in this country. It early became apparent to the phytosociologists that the size, number and distribution of quadrats influenced greatly the quantitative results obtained from a quadrat study of a given plant community.

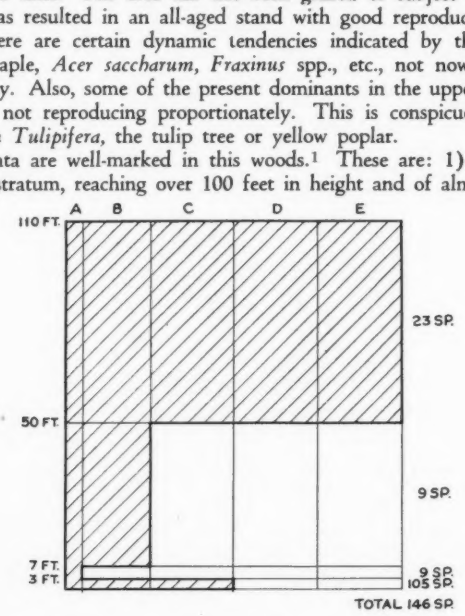
Even a cursory consideration would suggest that the minimum area for sample plots would depend on the nature of the community to be investigated. The use of quadrats of smaller size than the critically determined minimum area would give an inadequate sampling of the vegetation while the use of unnecessarily large quadrats would add materially to the labor of the investigation without increasing correspondingly the accuracy of the results. In spite of this rather obvious situation, practically nothing has been done on American plant communities in the way of a critical study of sampling methods. One recent contribution is a study of the size of list quadrats for use in grazing investigation, Hanson and Love (1930). The present study of sampling methods is published separately and in advance of a complete phytosociological analysis, Cain (1932), of Nash's Woods, which is one of several virgin forest relics now being studied by the writer.

A BRIEF DESCRIPTION OF THE WOODS

Nash's Woods lies in Sec. 2, Twp. 5, Range 13 W., about five miles east and south of New Harmony, Posey County, Indiana. This property has been in the hands of the Nash family, now owned by Mr. John Nash, for 117 years from its original settlement. The entire woods consists of

about 45 acres. The portion studied, about 25 acres, is old-aged, 15 acres of which are virgin, only a few dead and dying old trees having been removed from time to time. The area has not been grazed or subject to fire. This protection has resulted in an all-aged stand with good reproduction of some species. There are certain dynamic tendencies indicated by the abundance of young maple, *Acer saccharum*, *Fraxinus* spp., etc., not now conspicuous in the canopy. Also, some of the present dominants in the upper arborescent stratum are not reproducing proportionately. This is conspicuously true of *Liriodendron Tulipifera*, the tulip tree or yellow poplar.

Four strata are well-marked in this woods.[1] These are: 1) the superior arborescent stratum, reaching over 100 feet in height and of almost complete



COVERAGE CLASSES AND NUMBER OF SPECIES BY STRATA

Figure 1. This diagram, of a type introduced by European ecologists, serves to present graphically the number and height of the strata and at the same time to indicate the coverage class and the number of species involved in its formation.

coverage; 2) the inferior arborescent stratum, with a maximum height of about 50 feet, but with crowns of mature trees frequently only 30-40 feet high; 3) the shrub stratum, attaining a height of about seven feet and of low coverage; and 4) the "Feldschicht" of Du Rietz (1930b) composed of herbs, low shrubs and woody vines which trail rather than climb. Subdivision of this stratum is more or less evident, especially when seasonal aspects are considered. There is practically no "Bodenschicht" or soil stratum of mosses and lichens. These strata and their coverage classes are diagramed in figure 1 together with the number of species in each layer (exclusive of

1 The term "stratum" is used in translation of the German term "Schicht," rather than "layer" because of other uses of the latter term.

vernal species not represented in the summer). The photographs reproduced in figure 2 and figure 3 show various features of the stratification as well as the general aspect of the woods. The subterranean stratification has not been investigated but a knowledge of it is necessary for a complete picture of the structure of a complex plant community like a forest. The lowest stratum may reach class E coverage (76-100 per cent) as illustrated in figure 3 and consist almost entirely of woody vines as the poison ivy, *Rhus Toxicodendron,* and Virginia creeper, *Parthenocissus quinquefolia.* These two woody vines do not show as strong a tendency to climb as they usually do and it is difficult to find an explanation for their behavior.

Figure 2. An Exterior View of Nash's Woods in Early Spring. The flowering condition of *Cornus florida* serves to make distinct the height of the inferior arborescent stratum. Photograph by S. A. Cain.

Each of these strata behaves more or less like a separate community and they constitute dominance within dominance. The data presented in this paper do not show the situation as well as might be since the purpose is different, but in each stratum there is a small number of species which compose most of its coverage and which are to be considered the dominants for that stratum. Thinking in terms of crown cover, it is easy to conceive of each stratum as limited and their occurrence, one above another, like the floors in a building. Each stratum, however, has intimate relations with the ones below and is limited only above. The trunks and stems of the plants of each stratum occupy space in all lower layers. This would not be so only in the case of epiphytes which do not occur in this plant community. It is also to be remembered that reproduction, at different ages, occupies the

Figure 3. An Interior View of Nash's Woods in Summer. Members of three of the vegetational strata are here distinct. The large trees are *Liriodendron Tulipifera* of the superior arborescent stratum. The small tree in the center is a mature *Carpinus caroliniana* and the small tree on the left is *Cornus florida*, both of the inferior arborescent stratum. The ground layer is seen to be composed essentially of *Rhus Toxicodendron* and *Parthenocissus quinquefolia* of almost 100 per cent coverage to the exclusion of herbs. Photograph by S. A. Cain.

strata successively from the ground up to its mature height and constitutes a part of each stratum. Such immature plants of a higher stratum are called "transgressives" in any inferior stratum. Much of the dynamics of any complex piece of vegetation can be deduced from the comparative abundance of "key" species in the various strata. For example, *Liriodendron Tulipifera,* as previously pointed out, is an important dominant in the superior arborescent stratum but is practically absent in the lower strata as a transgressive, while *Fraxinus lanceolata* and *Ulmus fulva,* the slippery elm, are reproducing well and are important as transgressives in the lower strata. The potential future shift in the proportion of these species in the superior arborescent stratum is apparently evident, but another factor must be borne in mind, that of survival capacity of the different species at more advanced ages.

The superior arborescent stratum contains such species as *Liriodendron Tulipifera, Quercus alba, Nyssa sylvatica Fraxinus lanceolata, Ulmus fulva* and *Prunus serotina* which are of high frequency and considerable coverage, while the following are only represented by a few individuals and are relatively unimportant; *Quercus imbricaria, Q. borealis* var. *maxima, Q. rubra, Liquidamber styraciflua,* etc. Especially important in the inferior arborescent stratum are *Cornus florida,* (figs. 2, 3), *Carpinus caroliniana, Sassafras officinale* and *Cercis canadensis. Morus rubra, Asimina triloba, Celtis laevigata* and others are of lesser importance. The shrub stratum is represented by *Sambucus canadensis, Benzoin aestivale, Corylus americana, Viburnum prunifolium, Evonymus atropurpureus,* etc., none of which is of any appreciable coverage although the frequency of Benzoin is fairly high. As previously mentioned, *Rhus Toxicodendron* and *Parthenocissus quinquefolia* cover extensively in the ground stratum. Common herbs are *Geum canadense, Circaea latifolia, Arisaema triphyllum, Polygonum Virginianum, Pilea pumila, Laportea canadensis, Asarum canadense,* etc. As shown in figure 1 there are many species which enter this stratum. Some of the less common ones in the woods of the region are *Hydrastis canadensis, Panax quinquefolia, Pogonia trianthopora, Orchis spectabilis* and *Passiflora lutea.*

With these few remarks about Nash's Woods and the vertical structure of woodlands we are ready to consider the problem of analysis and especially the matter of quadrat sizes.

Methods

The first investigation was made on a basis of twenty-five sets of quadrats scattered evenly and widely over the extent of the woods studied. Two other sets were later employed. This first set, studied in June and July, 1932, consisted of twenty-five quadrats each of six different sizes: one, two, four, twenty-five, fifty and one hundred square meters. Each succeeding larger size contained the preceding smaller quadrats as shown in figure 4. The 150 quadrats were surveyed by means of a forest service staff compass and steel tape, and were staked out and enclosed by heavy white cord. A species list was made for each one meter quadrat. The additional species found in the second square meter, completing the two square meter plot, were added to the list. Again, the additional species in the two square meters

Figure 3. An Interior View of Nash's Woods in Summer. Members of three of the vegetational strata are here distinct. The large trees are *Liriodendron Tulipifera* of the superior arborescent stratum. The small tree in the center is a mature *Carpinus caroliniana* and the small tree on the left is *Cornus florida,* both of the inferior arborescent stratum. The ground layer is seen to be composed essentially of *Rhus Toxicodendron* and *Parthenocissus quinquefolia* of almost 100 per cent coverage to the exclusion of herbs. Photograph by S. A. Cain.

which formed, together with the smaller plots, the four square meter quadrat were added. This listing process was repeated for the twenty-five, fifty and one hundred square meter plots for each of the twenty-five sets. The data were assembled on one large chart with 110 horizontal columns for the total flora of the survey and twenty-five vertical columns for the sets of quadrats.

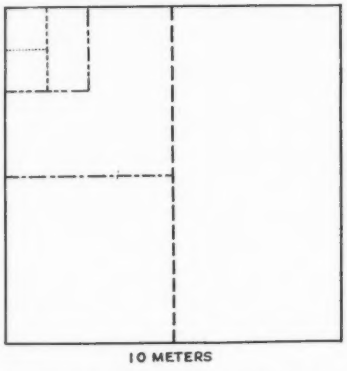


Figure 4. This diagram shows the system of the sets of quadrats investigated in June-July, 1932. Each larger size includes the smaller ones. These were 25 evenly and widely distributed sets of quadrats.

ARRANGEMENT OF QUADRATS

Species-Area Relationship

Tables 1 and 2 show the relationship between the size of the quadrat used in a survey and the average number of species per quadrat from a random sample (quadrats arranged in a checker-board design throughout the area) by means of 25 evenly and widely spaced quadrats of each size. The results of the first survey, June-July, 1932, appear together with those of later surveys. The average number of species per quadrat was found to increase rapidly at first with an increase of quadrat area, but to soon diminish in rate of increase. Figure 5.

The standard deviation and probable error of these means were figured to express the variability of the individual quadrats and to enable a statistical comparison of the means. The usual formulae were used except that $n\text{-}1$ was substituted for n, the number of quadrats being relatively small. The formulae follow:

$$\sigma = \sqrt{\frac{\Sigma D^2}{n\text{-}1}} \qquad (1)$$

$$M_E = 0.6745 \frac{\sigma}{\sqrt{n}} \qquad (2)$$

$$D_E = \sqrt{M1_E{}^2 + M2_E{}^2} \qquad (3)$$

Formula 1) is for the standard deviation (σ) in which (ΣD^2) equals the summation of the deviations squared of each sample from the mean of all samples. n is the number of quadrats used in the studies. Formula 2) is for the probable error of the mean (M_E). Formula 3) is for the probable error of the difference between two means (D_E), which is the square root of the sum of the squares of the probable errors of the two means.

TABLE 1

The relation between the size of the sample area and the average number of species per quadrat, from 25 evenly and widely distributed quadrats of each size.

Quadrat size	Survey of June and July, 1932	Survey of August and September, 1932	Survey of July 1933
1 sq. m. each	9.0 ±0.45	8.9 ±0.28	
2 sq. m. each	12.6 ±0.44	12.9 ±0.39	
3 sq. m. each		15.6 ±0.55	
4 sq. m. each	17.4 ±0.51	18.0 ±0.63	
9 sq. m. each			15.6 ±0.55
16 sq. m. each			21.2 ±0.70
25 sq. m. each	30.6 ±0.57		
50 sq. m. each	38.3 ±0.72		
100 sq. m. each	45.3 ±0.59		

TABLE 2

The value of the differences between the average number of species per quadrat from the different surveys.

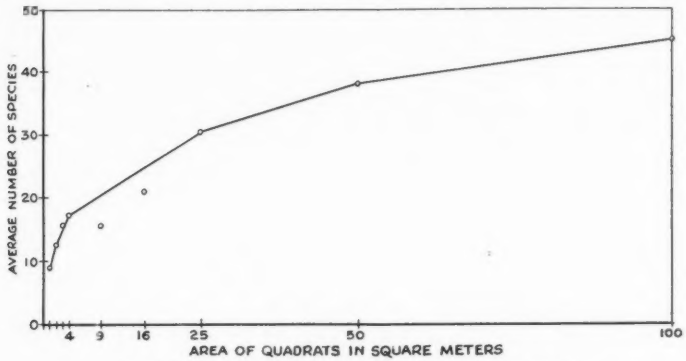
Surveys compared	p.e. of d. between different surveys	d. between averages	Statistical value of difference
1 with 2 sq. m.	±0.638	3.6 sp.	5.6
2 with 3 sq. m.	±0.704	3.0 sp.	4.2
3 with 4 sq. m.	±0.75	1.8 sp.	2.4
4 with 9 sq. m.	±0.75	1.8 sp.	2.4
9 with 16 sq. m.	±0.89	5.6 sp.	6.3
16 with 25 sq. m.	±0.902	9.4 sp.	10.4
25 with 50 sq. m.	±0.918	7.7 sp.	8.4
50 with 100 sq. m.	±0.931	7.0 sp.	7.5
1 with 1 sq. m.	±0.53	0.1 sp.	0.2
2 with 2 sq. m.	±0.59	0.3 sp.	0.5
4 with 4 sq. m.	±0.65	0.6 sp.	0.8

THE MINIMUM AREA CONCEPT AND RELATIONSHIP TO FREQUENCY AND CONSTANCY

The purpose of this investigation was essentially to determine a method for the minimum quadrat area for sampling such a woods as Nash's Woods, but, we immediately become involved in several established and somewhat divergent concepts, as local constance, general constance, frequency, minimum area in the sense of the north-Europe sociologists (the Minimiareal—DuRietz, 1930) and in the sense of the Swiss sociologists (the Minimalraum—Braun-

Blanquet, 1932; Braun-Blanquet and Jenny, 1926), which have to be explained and interpreted.

The Minimiareal of DuRietz is founded on the practice of distinguishing constants, accessory and accidental species. The concept of constance was advanced by Brockmann-Jerosch (1907) although Cajander (1904) had established the closely related concept of presence somewhat earlier. DuRietz and his associates have been largely responsible for the development of the idea of constant species and their importance in community identification



RELATION OF AVERAGE NUMBER OF SPECIES PER PLOT TO SIZE OF PLOT

Figure 5. This curve breaks most strongly at the 4 square meter size and this is taken to indicate that size as the minimum area for quadrats under the given conditions.

and minimum area determination. Brockmann-Jerosch distinguished between "constant" species, those occurring in more than one-half of the lists of plants taken from several association individuals (stands); "accessory" species, noted in one-fourth to one-half of the lists; "accidental" species figuring in less than one-fourth of the lists. One sample plot per stand is employed for general constance. Braun-Blanquet with five groups of constance designates those species above 80 per cent as "constant," while DuRietz, with ten groups, designates his last group of species, 90-100 per cent, as "constant." For constance determination they all hold that the stands investigated must be fully developed and internally as uniform as possible, and that collectively they must be representative of the community in the abstract—that is, springing from a not too small region of investigation. This results in general or regional constance for the community type. In order to be sure that one has always the constant species of the community type falling in the quadrat it must not be too small. It needs a minimum area, called "minimiareal." As Rübel (1930) says, "the minimiareal is a measure of the average individual distance of the constants of the community which stand farthest from one another." This idea originated from Palmgren (1922), "Das Minimi-

areal der Assoziation ist ein Mass für den mittleren Individuenabstand der am weitesten auseinanderstehenden Konstanten."

Romell (1925) says that "In reality, in natural associations, the number of constants increases at first rapidly with increase in size of the sample areas, but soon becomes practically constant or shows increase at least very slowly." He continues to add that, the number of constants depends upon the size of the areas, also on their number and that the course of the curve, expressing the constancy-area relationship can change with the number of sample areas. Kylin (1926) and Nordhagen (1922, quoted by Lippmaa 1933) have established from the standpoint of principle there is to be regarded no difference between these groups of species (constant, accessory, and accidental species). As Lippmaa says, "The number of constants an association contains depends on the size of the quadrant used. There is no small surface area from which the number of constants does not further increase, also no minimiareal is possible in the sense of DuRietz."

Markgraf (1926) in his "Kleines Praktikum der Vegetationskunde" gives an illustration of constance and minimiareal determination for the *Polytrichum strictum*-association of the hochmoor near Berlin. He employs ten different stands and uses in each a four sq. m. quadrat (10 quadrats); divides these into one sq. m. quadrats (40 quadrats) and one each of these into one-fourth sq. m. quadrats (40 quadrats). The constant species (90-100 per cent) for the forty one-fourth sq. m. quadrats were *Polytrichum strictum, Vaccinium oxycoccos, Drosera rotundifolia* and *Sphagnum acutifolium.* The forty one sq. m. quadrats added the following two constant species: *Sphagnum cymbalifolium* and *Eriophorum vaginatum,* while the ten four sq. m. quadrats made no additions to the list of quadrats. Markgraf concludes that the one sq. m. quadrat is the minimiareal since the larger quadrats added no new species to the list of constants. But this method is obviously faulty—how could the ten four sq. m. quadrats and the forty one sq. m. quadrats differ in the number of constants, they are identical areas (the former containing the latter). If he had employed only ten one sq. m. quadrats and ten one-fourth sq. m. quadrats, as he did for the largest area; or had used forty different stands with one area of each size in a stand, he would have had a valid basis for his constancy-area determination. One can but suppose that under the conditions suggested the larger area would have contributed some new constants to the list.

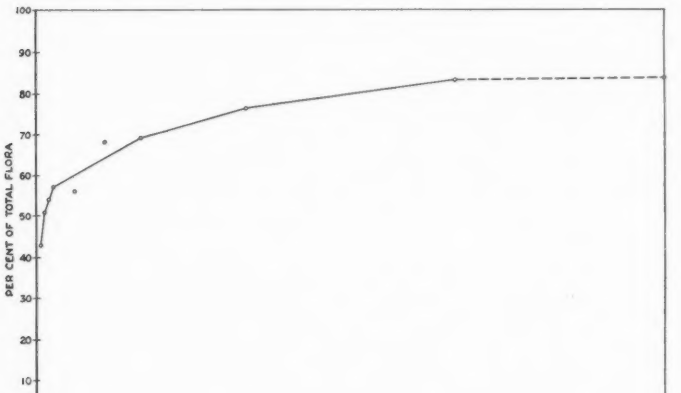
The difference between the constance for a community type of a region (that described above) and that for a stand (Lüdi 1928) is completely correct. Constance within a stand (association individual) is not different from frequence is the sense of Braun-Blanquet (1928, 1932), in so far as the author can discern, and will be discussed later.

If the minimiareal concept fails, it is not so with the *minimalraum* of Braun-Blanquet (loc. cit. and 1926), which is the smallest area necessary for an association in a definite locality to exhibit its special species (its characteristic, and attendant species. See the discussion of fidelity by Braun-Blanquet 1928 and 1932, and Cain 1932). It is determined practically by means of the species-area curve. Lippmaa (1933) says that "In so far as a

change is necessary in the method of Braun-Blanquet it is for the final determination of minimalraum in which the accidental species (based on fidelity) should not be counted, as they belong to other associations." The size of the minimalraum is as characteristic a feature of an association as the floristic assemblage and the number of species of the individual association.

In the curves showing the relationship between species and area either the mean number of species on each quadrat size or the percentage, the species from each survey are of the floristic assemblage, are plotted against the quadrat size (on the x-axis). These determinations are based on one quadrat of each size in each of several association individuals, usually ten or more stands being used as described for minimiareal determination.

If the same method is employed, i.e. scattering sample plots of different size but within an association individual, the results will give frequency of the species, the average number of species per quadrat of each size (figure 5), and the total number of species from all quadrats of one size (Table 3 and figure 6). These data can be plotted against area to produce curves similar to constancy curves and minimalraum curves. Thus one can designate the species of high frequency (Raunkiaer's class E, 80-100 per cent) within the association individual as the "local constants" in distinction to general constants. It is better, however, to retain Braun-Blanquet's terminology (1928). One can also employ the shape of the curves obtained to determine the minimum quadrat area for sampling an association individual (Hanson and Love 1930). The sample plot area at which the curves flatten strongly is taken to be the minimum quadrat area.



RELATION OF TOTAL NUMBER OF SPECIES PER SURVEY TO AREA SAMPLED

Figure 6. This curve also breaks most strongly at the 4 square meter size. (See figure 5).

TABLE 3

The relation between the total number of species and the size of the sample plot and the manner of distribution.

Area	Arrangement	Number of species	Per cent of total flora	Per cent of total area
25 sq. m.	scattered in 1 sq. m. plots	57	43	.025
50 sq. m.	scattered in 2 sq. m. plots	67	51	.050
75 sq. m.	scattered in 3 sq. m. plots	72	54	.075
100 sq. m.	scattered in 4 sq. m. plots	75	57	.100
225 sq. m.	scattered in 9 sq. m. plots	74	56	.225
400 sq. m.	scattered in 16 sq. m. plots	90	68	.4
625 sq. m.	scattered in 25 sq. m. plots	91	69	.625
1250 sq. m.	scattered in 50 sq. m. plots	100	76	1.25
2500 sq. m. .62 acres	scattered in 100 sq. m. plots	110	83	2.5
2023 sq. m. .5 acres	in one plot	74	57	2.0
100,000 sq. m. approximately	total woods 25 acres approximately	132	100	100.0

Frey (1927) discussed the use of such curves (which were introduced by Jaccard) in plant sociology and in 1928 elaborated on his discussion of the literature and its significance. He states, "It is understandable that the species-area curve must eventually approach the horizontal because the region investigated can finally become larger without the corresponding appearance of several new species. It is inherent, but not usually stated, that the reduction of species increase must ever and above all follow the rule of a horizontal parabola (Arrhenius 1920, 21, 22) and when one charts Arrhenius' fundamental data on logarithmic paper, instead of a horizontal parabola, it yields a straight line." (See also, Jaccard 1902, 1908, 1928). The formula of Arrhenius is valid in consideration of extensive regions with diverse ecological conditions where there is the possibility that new species will be met with continually. This is also especially true of the formula of Romell (1925) where regions are studied without reference to plant communities. Gleason (1922, 1925) has criticized Arrhenius' formula and demonstrated that it gives far too high figures when applied to areas of considerable size. Gleason found that the number of species varied as the logarithm of the area, rather than directly, subject also to an exponential number (factor) which determines the pitch of the curve. Frey (1928) continues, "When we investigate the species-area relationship within an association the saturation curve is expected, for with definite ecological conditions are united a definite group of plants limited in number." Such a curve, the so-called saturation curve, ascends rapidly at first and with increasing surface area quickly becomes parallel with the x-axis. It is fundamentally different from that of Arrhenius. The formula for it has been given by Kylin (1926) and on logarithmic paper the curve is concave over the x-axis. This curve corresponds to the data of Du-Rietz whose species-area curves of "constants" are saturation curves *par*

excellence. In the investigation of the *Curvuletum* of the high Alps Braun-Blanquet and Jenny (1926, p. 265) found typical saturation curves. The curves of Hanson and Love (1930) on *Agropyron Smithii* mixed prairie are not of this type but of the parabolic type. Of the curves in the present paper, figure 6, giving the per cent of the total flora for each quadrat size is closest to the saturation curve type; figure 7, of the average frequency of species is intermediate; and figure 5, of the average number of species per plot is more nearly of the parabolic type.

When surveys involving the same size and number of quadrats but made at different times and with a different distribution through the woods are compared, as in the bottom of table 2, it is seen that there is absolutely no difference of statistical value, i.e. the differences would commonly occur in random sampling. It is commonly accepted that a difference must be more than three times the probable error of the difference (see formula 3) at which the chances are about twenty-two to one that the difference is not due to chance but, in this case to the quadrat size.

From table 3 it is apparent that the practice of scattering the total area sampled in several quadrats, rather than in one or a few larger plots, is of great value in such investigations. The twenty-five one sq. m. plots contained 43 per cent of the total flora although only 0.025 per cent of the area. A scattered sampling of 0.1 per cent of the area gives 57 per cent of the total flora while the use of the largest size of plot (100 sq. m. each) gives 83 per cent of the flora on a basis of 2.5 per cent of the area. A single sample plot of 2.0 per cent of the area (0.5 acres) is very inadequate in comparison with the scattered plots of about equal total acreage. In fact, as many species composed the floristic assemblage when obtained by a survey of one-twentieth the area of the half-acre plot as when twenty-five scattered quadrats were used.

The curves in figures 5 and 6 can be taken to indicate that a quadrat of four sq. m., if twenty-five of them are used, would be adequate for sampling the woods, since the strongest breaks in the curves come at that area, although a larger size, if time permitted, would be better. This indication must not be too strongly relied upon, however, for two reasons. In the first place the woods was studied as a whole, without separate sampling for the various strata; and in the second place no study was made of the influence of a greater number of quadrats. Obviously such small sized quadrats would be of little value in giving the details of the arborescent stratum. It is seldom, however, that a mature tree occurs near a quadrat without also being represented by reproduction of various ages in the quadrat, or at least by coverage, if not by rooted individuals. From the point of view of frequency data and species-area relationships the apparently small quadrat size still has a modicum of validity for the superior strata, and indubitable validity for the woods as a whole. It is admitted freely that the present sampling is far from the best (see the following section on the woods as an association) but it has served to test certain methods and concepts. In general it can be said, the larger the number of species in a vegetation type and the smaller the number of codominants in the strata (when the species are numerous), the greater the heterogenity of the community and the more difficult the analysis becomes.

A Consideration of Hanson and Love's Frequency Ratios

The frequency of a species, according to phytosociological concepts, is the number of quadrats in which a species is encountered, expressed in per cent of the total number of quadrats used in the survey. The density, per se, of a species is not considered in this connection, but rather, its evenness of distribution, since it has to be reperesented by only one individual per quadrat to have a frequency of one hundred per cent. Table 4 gives the frequency per cent of each of the species in the six early summer surveys, 1932. The total floristic list for the one meter survey consisted of 57 species, the two square meter survey listed sixty-seven species, etc., up to 110 species for the survey using 100 square meter quadrats. From a study of the table it becomes apparent that the frequency per cent for any one species tends to increase as the size of the sample plot is increased, up to 100 per cent frequency after which there would be only a density increase. This is to be expected since each larger sample area would normally contain more species, as shown previously. It would follow that any one species would have a better chance of occurring in any one sample plot, and consequently have a higher frequency for its total occurrence in all the plots of the survey. Gleason (1925) has remarked, "A high frequency index requires a large number of individuals, and it is generally true that the number of individuals of any species is an indication of the degree of adaptation to the environment."

In an effort to employ frequency data from these surveys to determine which of these sizes is most suitable for sampling such a piece of vegetation as Nash's Woods, a method employed by Hanson and Love (1930) on their study of comparative quadrat sizes in grazing areas was used. It may be said at first that this rather involved method seems to be unsound in some of its aspects and that it is certainly unnecessarily tedious as will be explained later. Their procedure and certain criticism of it are presented here to reopen the matter as the present writer may have been unable to derive some utility which the method may contain. This may also serve to prevent future workers on the problem of statistical methods in vegetation from laboring over a futile mathematical manipulation. Following is a description of the analysis of the Nash's Woods data after the method of Hanson and Love (loc. cit.) For each species and for each size of quadrat, table 4, the frequency of the species was divided by its frequency in the next larger of the quadrat sizes. For example, *Acer saccharum* has a frequency of 56 per cent in the one sq. m. quadrat survey and a frequency of 76 per cent in the two sq. m. quadrat survey. Therefore, 56/76 equals 0.737, which is the ratio of the relationship. In order to weight this relationship it was multiplied by the number of quadrats in which the species occurred in the larger of the two sizes, in this case by 19. This gave for *Acer saccharum* a weighted ratio of 14.0 for the frequency relationship of the species in the two sizes of quadrats.[1]

[1] This weighted ratio is simply the number of quadrats in which the plant occurred, using the smaller of the two quadrat sizes. The mathematical manipulation brings one round a circle.

The next step was to compare the results of one survey with those of another. The weighted ratios for all species in one size of quadrat were added. This was repeated for each size. The number of quadrats in which each species occurred in the next larger size of quadrat was added. The sum of the weighted ratios was divided by the sum of the frequency numbers (quadrat numbers not percentage). This gave the *weighted average ratio*, expressing the relationship of each frequency survey to the next using a larger size of quadrat. As a final step, these ratios, table 5, were added and the *average* weighted average ratio was determined. For the six surveys this was 0.677. This ratio lies between the ratio derived by comparing the four sq. m. quadrat survey with the twenty-five sq. m. quadrat survey, and that derived by comparing the twenty-five sq. m. quadrat survey with the fifty sq. m. quadrat survey. It is, however, also close to the ratio derived from a comparison of the one sq. m. survey with the two sq. m. survey. Since this latter ratio is out of the series formed by the others it is here considered anomalous. Also, due to the larger size of the quadrats from which the other corresponding ratio was derived (the one centering on the twenty-five sq. m. quadrat) it would apparently be more sound.

TABLE 4

Frequency of species from 25 quadrats each of six sizes. Survey of June-July, 1932.

Floristic list[1]	Frequency per cent: Quadrat sizes 1-m	2-m	4-m	25-m	50-m	100-m
TREES						
Acer Negundo L.		4	4	28	40	52
A. saccharum Marsh.	56	76	100	100	100	100
Asimina triloba (L.) Dunal	12	16	16	44	60	68
Carpinus caroliniana Walt.	8	12	12	48	60	64
Carya cordiformis (Wang.) K. Koch	4	8	12	52	64	76
C. glabra (Miller) Sweet	4	12	24	48	56	68
C. laciniosa (Michx.f.) Loud		4	8	12	20	24
Celtis laevigata Willd.					4	8
C. occidentalis L.	4	12	12	20	36	40
Cercis canadensis L.	20	32	40	64	64	64
Cornus florida L.	24	28	32	60	72	84
Fraxinus Biltmoreana Beadle	4	4	8	16	24	28
F. lanceolata Borck.	52	72	76	96	100	100
Gleditsia triacanthos var. *inermis* Pursh.				4	4	4
Gymnocladus dioica (L.) K. Koch						4
Juglans cinerea L.			12	16	20	24
J. nigra L.			4	8	8	12
Liquidamber styraciflua L.					16	24
Liriodendron Tulipifera L.	8	16	24	56	68	80
Morus rubra L.	4	8	8	40	56	76
Nyssa sylvatica Marsh.	20	24	24	60	86	80
Prunus serotina Ehrh.	4	8	32	60	80	88
Quercus alba L.			8	16	24	40
Q. borealis var. *maxima* (Marsh.) Ashe	4	4	8	28	48	56
Q. imbricaria Michx.					4	4

1 I wish to thank Mr. Charles C. Deam for assistance in certain nomenclatural matters but I am entirely responsible for any errors which may be present.

Floristic list	Frequency per cent: Quadrat sizes 1-m	2-m	4-m	25-m	50-m	100-m
Q. Prinus L.				20	32	60
Sassafras officinale Nees & Eberm.	16	44	48	72	88	88
Ulmus fulva Michx.	24	32	52	76	76	92
SHRUBS						
Ampelopsis cordata Michx.	12	16	32	60	68	68
Benzoin aestivale (L.) Nees	4	4	28	68	72	72
Campsis radicans (L.) Seem.						4
Celastrus scandens L.	4	4	4	24	32	36
Corylus americana Walter	4	4	4	12	16	20
Evonymus atropurpureus Jacq.		8	12	36	44	60
Menispermum canadensis L.	4	4	8	28	48	56
Parthenocissus quinquefolia (L.) Planchon.	44	80	92	100	100	100
Rhus Toxicodendron L.	56	68	80	96	96	100
Rubus argutus Link.						4
Sambucus canadensis L.	4	8	16	56	60	76
Smilax hispida Muhl.	20	24	32	64	80	92
Solanum Dulcamara L.	4	12	12	12	16	16
Symphoricarpos orbiculatus Moench.				16	24	40
Viburnum prunifolium L.				4	4	16
Vitis aestivalis Michx.	4	4	8	24	28	48
FERNS						
Athyrium acrostichoides (Sw.) Diels.						4
A. angustifolium (Michx.) Milde					4	4
Botrychium ternatum f. *obliquum* Milde					4	4
B. virginianum (L.) Sw.		4	8	24	48	76
Onoclea sensibilis L.			4	4	4	4
Polystichum acrostichoides (Michx.) Schott.						4
Thelypteris hexagonoptera (Michx.) Weatherby			8	24	44	60
HERBS						
Actea alba (L.) Mill.					4	8
Agrimonia mollis (T&G) Britton	8	16	28	32	52	56
Ambrosia elatior L.				4	8	12
A. trifida L.				4	4	4
Arisaema Dracontium (L.) Schott.	12	24	24	60	80	88
A. triphyllum (L.) Schott.	28	44	76	96	100	100
Asarum canadense L.	20	20	24	40	40	48
Blephilia hirsuta (Pursh) Benth.						20
Carex spp.	56	64	84	92	96	96
Circaea latifolia Hill	36	36	40	56	68	72
Clematis virginiana L.					8	12
Collinsonia canadensis L.	8	12	24	32	36	48
Corallorrhiza maculata Raf.				4	4	4
Cynoglossum virginianum L.	12	16	16	28	40	64
Dentaria diphylla Michx.						4
Desmodium grandiflorum (Walt) DC.	8	16	28	48	56	56
Dioscorea villosa L.	8	12	28	56	76	84
Erigeron philadelphicus L.	4	4	4	8	12	12
Galium concinnum T. & G.	4	4	20	36	40	44
G. triflorum Michx.	24	28	28	52	68	72
Geranium maculatum L.	4	4	12	12	28	36

Floristic list	Frequency per cent: Quadrat sizes 1-m	2-m	4-m	25-m	50-m	100-m
Geum canadense Jacq.	20	36	36	72	84	92
Hackelia virginiana (L.) Johnson	4	8	8	8	8	32
Hydrastis canadensis L.				4	8	20
Impatiens pallida Nutt.	12	16	16	28	36	40
Lactua canadensis L.			4	12	16	20
L. scariola L.				4	4	4
Orchis spectabilis L.					4	4
Osmorhiza Claytoni (Michx.) Clark				4	4	4
O. longistylis (Torr.) DC.				4	4	8
Oxalis cymosa Small	4	12	16	28	44	52
Panax quinquefolia L.				4	12	16
Panicum sp.?	4	4	4	8	24	32
Parietaria pennsylvanica Muhl.			4	4	16	24
Passiflora lutea L.				4	4	4
Phlox divaricata L.	12	20	24	36	40	44
Phyrma Leptostachya L.	12	20	20	44	48	48
Phytolacca decandra L.		8	8	16	32	32
Pilea pumila (L.) Gray	24	32	40	56	60	60
Poa sylvestris ??*	8	8	8	40	44	44
Podophyllum peltatum L.	4	8	12	12	20	36
Polemonium reptans L.					8	16
Polygonum scandens L.			8	12	36	44
P. Virginianum L.	8	12	20	36	48	68
Prenanthes alba ??*				4	4	8
Ranunculus recurvatus Poir.		4	4	16	24	32
Ruellia carolinensis (Walt.) Steud.		4	8	8	8	8
Sanguinaria canadensis L.						4
Smilacina racemosa (L.) Desf.			8	8	12	20
Trillium Gleasoni Fernald						4
T. recurvatum Beck.		4	12	32	36	40
Urtica procera Muhl.	8	16	24	52	72	80
Uvularia grandiflora Smith			4	4	4	4
Veronia sp.?*				4	4	8
Viola papilionacea Pursh.	68	72	76	80	84	96
V. striata Ait.	16	24	28	44	44	48
?*		4	4	12	16	16
??*				4	4	4
???*						4
Number of species	56	65	75	91	100	110
Average species frequency	15.4	19.5	23.2	33.7	38.4	41.1

* Young vegetative material, unidentifiable.

Another set of quadrats was taken for a similar analysis which provided a check on the discrepancy of the first ratio. This investigation was made two months later in 1932 but with quadrats located differently. The data are presented in table 6 for quadrat surveys employing 1, 2, 3, and 4 sq. m. sizes. These frequency percentages were treated as described in the preceding paragraphs and gave a second set of weighted average ratios which are also found in table 5. This group of ratios forms a progressive series in which

the first ratio takes a normal position. It would be concluded, following Hanson and Love (1930, p. 577) that the twenty-five square meter quadrat size is adequate for sampling such a woods when (twenty-five quadrats are used). Writing of their results on grassland vegetation, they say, "Since these ratios are between 1 and 2 square meter sizes the conclusion may be drawn that the size to use in comparing the vegetation should not be smaller than 1 square meter." The author can not see that this conclusion is sound since the average weighted ratio, which is used to indicate the minimum adequate quadrat size, is a direct result of the range in quadrat sizes employed in the comparison. If only the smaller quadrat sizes are investigated and their weighted average ratios obtained the average weighted average ratio would be smaller than the size indicated. If only larger plots were used the average, and hence the mimimum area for sampling, would be larger, and so on with any variation. It would seem that the method of frequency ratios is useless in the present form of treatment.

In searching for some method of utilizing data of species frequency for indication of minimum quadrat size, the writer struck on the simple method of determining average frequency of all species for each survey in which a different size of quadrat is used. These average frequencies plotted with area in the manner of the other curves produces a curve, figure 7, which is similar to the preceding. These average species frequencies, based on all species in each survey, are given in table 7. The same data may also be treated in another manner, as follows: Determine the percent of average species frequency increase on a basis of the increase in area. Such calculations give the following results: a) Increase of plot size from one to two sq. m. resulted in an average increase of species frequency of 4.1 per cent; b) from two to four sq. m. gave an increase of 1.85 per cent; c) from four to twenty-five gave 0.5 per cent; d) from twenty-five to fifty gave 0.19 per cent; and e) from fifty to 100 sq. m. have only 0.05 per cent. When plotted these figures also give a curve which breaks strongly at the four sq. m. size.

TABLE 5

Weighted average ratios expressing relationship of frequencies of each size of quadrat to the next larger size.

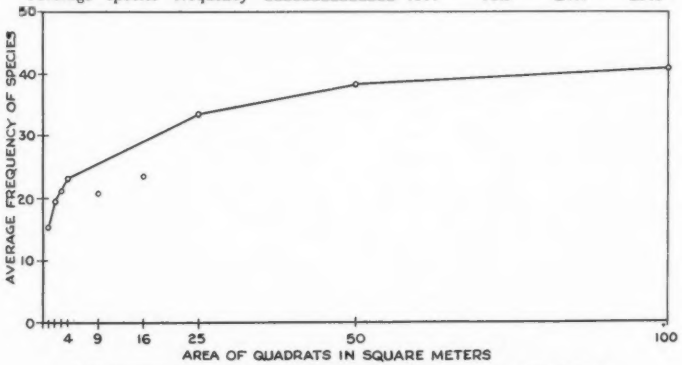
Quadrat sizes in square meters	Ratios from two surveys	
	June 30-July 8, 1932	Aug. 30-Sept. 1, 1932
1 with 2 sq. m.	0.685	0.692
2 with 4 sq. m.	0.482	0.701
2 with 3 sq. m.		0.836
3 with 4 sq. m.		0.861
4 with 25 sq. m.	0.576	
25 with 50 sq. m.	0.815	
50 with 100 sq. m.	0.825	
Average	0.677	

TABLE 6

Frequency of species from 25 quadrats each of four sizes. Survey of August-September, 1932.

Floristic list	Frequency per cent: Quadrat sizes 1–m	2–m	3–m	4–m
Acer saccharum Marsh.	52	72	76	84
Asimina triloba (L.) Dunal.	12	12	12	16
Carpinus caroliniana Walt.	16	24	28	28
Carya cordiformis (Wang.) K. Koch	4	16	24	32
C. glabra (Mill.) Sweet	12	16	24	28
C. laciniosa (Michx. f.) Loud.				4
Celtis laevigata Willd.		4	4	8
C. occidentalis L.		8	8	8
Cercis canadensis L.	4	8	12	16
Cornus florida L.	16	16	28	36
Fraxinus Biltmoreana Beadle	4	8	8	12
F. lanceolata Borck.	56	76	84	88
Liquidambar Styraciflua L.			4	4
Liriodendron Tulipifera L.		4	4	4
Morus rubra L.	4	8	8	8
Nyssa sylvatica Marsh.	16	32	36	44
Prunus serotina Ehrh.		12	28	36
Quercus alba L.	8	12	16	16
Q. borealis var. *maxima* (Marsh.) Ashe	4	12	16	20
Q. Prinus L.	16	16	16	24
Q. rubra L.		4	4	4
Sassafras officinale Nees and Eberm	32	40	48	60
Ulmus fulva Michx.	28	40	52	56
SHRUBS				
Ampelopsis cordata Michx.	16	28	40	44
Benzoin aestivale (L.) Nees	4	20	32	40
Celastrus scandens L.	8	20	24	28
Corylus american Walter	8	12	12	12
Evonymus atropurpureus Jacq.	4	4	4	8
Menispermum canadense L.	12	12	16	16
Parthenocissus quinquefolia (L.) Planchon	84	88	96	100
Rhus Toxicodendron L.	88	88	88	88
Rubus argutus Link.			4	4
Smilax hispida Muhl.	8	8	12	12
Viburnum prunifolium L.		4	4	4
Vitis aestivalis Michx.	8	12	12	12
FERNS				
Athyrium acrostichoides (Sw.) Diels	4	4	4	4
A. angustifolium (Michx.) Milde	4	4	4	4
Botrychium virginianum (L.) Sw.	4	16	16	16
Cystopteris fragilis (L.) Bernh.	4	4	4	4
Thelypteris hexagonoptera (Michx.) Weatherby	12	12	16	16
HERBS				
Agrimonia mollis (T. & G.) Britton	28	32	32	32
Apios tuberosa Moench.	4	4	4	4
Arisaema triphyllum (L.) Schott.	4	24	28	36
Asarum canadense L.	28	32	32	32
Campanula americana L.	4	8	8	8
Carex spp.	40	56	56	60
Circaea latifolia Hill	12	20	24	28

Floristic list	Frequency per cent: Quadrat sizes 1–m	2–m	3–m	4–m
Cynoglossum virginianum L.	8	8	12	12
Desmodium grandiflorum (Walt.) DC.				8
D. nudiflorum (L.) DC.		4	4	4
D. pauciflorum (Nutt.) DC.		4	8	16
Dioscorea villosa L.	12	12	12	36
Elephantopus carolinianus Raeuschel	4	4	8	8
Galium circaezans Michx.	8	12	16	24
G. concinnum T. & G.	32	32	32	36
G. triflorum Michx.	4	8	12	16
Geranium maculatum L.	8	8	8	12
Geum canadense Jacq.	24	28	40	52
Hydrastis canadensis L.		4	4	8
Lactuca canadensis L.		8	8	8
Laportea canadensis (L.) Gaud.	16	16	20	20
Orchis spectabilis L.	4	4	8	8
Oxalis cymosa Small	4	4	8	8
Phlox divaricata L.	12	28	32	32
Phryma Leptostachya L.	4	8	20	20
Pilea pumila (L.) Gray	20	24	36	40
Poa sylvestris ?	12	12	16	24
Parietaria pennsylvanica Muhl.			4	4
Pogonia trianthopora (Sw.) B. S. P.		4	4	4
Polygonum Virginianum L.	8	12	16	16
Ranunculus recurvatus Poir.	4	4	8	8
Silene stellata (L.) Ait.	4	8	8	8
Smilacina racemosa (L.) Desf.				8
Viola papilionacea Pursh	24	52	52	56
V. striata Ait.	8	16	24	24
Number of species	58	69	72	75
Average species frequency	15.4	18.5	21.1	23.6



RELATION OF AVERAGE FREQUENCY OF ALL SPECIES TO SIZE OF PLOT

Figure 7. This utilization of frequency data seems to be sound and results in a curve similar in all respects to the earlier ones. Again the strongest tendency to flatten is at the four square meter size.

TABLE 7

The average frequency based on all species in a particular survey.

Quadrat size	Survey of June-July, 1932	Survey of Aug.-Sept., 1932	Survey of July, 1933
1 sq. m.	15.4	15.4	
2 sq. m.	19.5	18.5	
3 sq. m.		21.1	
4 sq. m.	23.2	23.6	
9 sq. m			20.8
16 sq. m.			23.5
25 sq. m.	33.7		
50 sq. m.	38.4		
100 sq. m.	41.1		

RAUNKIAER'S LAW OF FREQUENCY

The frequency percentages of the species encountered in a quadrat survey are placed in classes. Sometimes ten classes are used but usually only five classes are employed: Class A, consists of species of 1 to 20 per cent frequency; Class B, 26 to 40; Class C, 41 to 60; Class D, 61 to 80 and Class E, 81 to 100 per cent frequent. When this has been done the number of species in each of the classes, usually expressed as per cent of the total floristic list, becomes of interest. In nearly all surveys, Class A is found to be very much larger than the others, that is, there are more species of a low frequency (1-20%) than of any other class of frequency. Normally the number of species in each successively higher frequency class becomes less with the exception of Class E which shows an increase. Raunkiaer's "normal" curve based on a large number of surveys shows the following distribution through the frequency classes: Class A, 53 per cent; Class B, 14 per cent; Class C, 9 per cent; Class D, 8 per cent and Class E, 16 per cent. These percentages plotted as a curve give a J-shaped curve which looks like part of a parabola. Kenoyer's (1927) results also give this form of curve but with Class A very much larger and Class E relatively smaller but still with a secondary peak. The differences are explained on a basis of the greater richness in species of the American flora. Our present interest is in the form of the curve and the possible value it may have in the interpretation of the present surveys by use of different sized quadrats.

Table 8 gives the frequency class percentages for twelve different surveys representing nine different quadrat sizes, three of the smaller sizes being duplicated. When these percentages are examined it is apparent that an increase in size of the sample plot employed produces a reduction in the number of species which fall in Class A. That is to say, the larger the sample area the smaller the percentage of species of low frequency since, as explained earlier, an increase in area produces an increase in the number of species falling in the plot. At the same time an increase in the size of the sample area produces an increase in the number of species of high frequency for the same reason. In table 8 it may be seen that the per cent of the floristic list falling in Class A for the one square meter plot is 78.8. There

TABLE 8

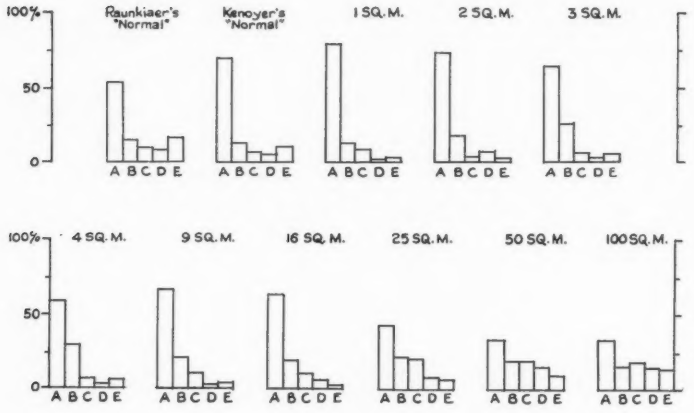
A comparison of frequency class percentages from surveys by means of different sized quadrats, twenty-five quadrats each.

Size of quadrat	Dates of survey	Frequency classes: per cent of flora F-1 A	F-2 B	F-3 C	F-4 D	F-5 E	Number of species
1 sq. m.	6/32	78.6	10.7	9.1	1.6	0.0	56
	8/32	79.0	13.0	4.0	0.0	4.0	58
	Average	78.8	11.8	6.5	0.8	2.0	57
2 sq. m.	6/32	70.8	17.0	3.2	9.0	0.0	65
	8/32	74.0	17.0	3.0	3.0	3.0	69
	Average	72.8	17.0	3.1	6.0	1.5	67
3 sq. m.	8/32	64.0	25.0	5.0	2.0	4.0	72
4 sq. m.	6/32	57.3	30.6	2.6	5.3	4.2	75
	8/32	60.0	25.0	9.0	0.0	6.0	75
	Average	58.6	27.8	5.8	2.6	5.1	75
9 sq. m.	7/33	66.2	20.2	9.4	1.5	2.7	74
16 sq. m.	7/33	63.3	18.8	10.0	5.5	2.2	90
25 sq. m.	6/32	42.8	22.0	21.0	7.7	6.5	91
50 sq. m.	6/32	38.0	19.0	19.0	15.0	9.0	100
100 sq. m.	6/32	38.1	15.4	18.1	14.5	13.6	110
Raunkiaer's "normal"		53.0	14.0	9.0	8.0	16.0	
Kenoyer's "normal"		69.0	12.0	6.0	4.0	9.0	

is a constant reduction of this figure until the 100 square meter plots produce only 38.1 per cent of the species of Class A frequency. In Class E the percentage rises from two in the one square meter plot to 13.6 in the 100 square meter plot survey. Surveys of increasingly smaller area of quadrats would augment Class A, Cain (1932) while the use of larger quadrats would augment the classes of higher frenquency. Gleason (1929), one may interpret, concludes that if all classes of frequency are represented and a secondary peak is present in Class E, it may be assumed that the sampling of the vegetation is adequate to show the frequency of the component species. Gleason (1929) says, "In conclusion we may say that Raunkiaer's law is merely an expression of the fact that in any association there are more species with few individuals than with many, that the law is most apparent when quadrats are chosen of the most serviceable size to show frequency, and that it is obscured or lost if the quadrats are either too large or too small." We may, with some reasonableness assume that the frequency curve which most nearly conforms to a normal shape indicates the survey, i.e. the quadrat size, best suited for analysis of the particular piece of vegetation investigated and probably for the whole type.

The frequency charts for the present studies are shown in figure 8 together with the "normals" of Raunkiaer and Kenoyer (1927). Some workers think the form of the curve significant as to vegetational structure while others think it a mathematical result of the method of sampling. To prove the mathematical significance of the curve would be a problem in itself.

Since the secondary peak in Class E appears in Raunkiaer's and Kenoy-



COMPARATIVE FREQUENCY CLASS PERCENTAGES OF NASH'S WOODS

Figure 8. These diagrams show graphically the effect on frequency classes of utilization of different sizes of sample areas. The so-called "normals" of Raunkiaer and Kenoyer are included.

ers averages (based on 8,087 and 1425 percentages, respectively) and in a large number of their individual surveys of plant communities, it is possible that any set of samples which yield similar percentages is better than a set which does not. This conclusion, however, is subject to question and more study is needed. These comparisons serve to emphasize one very important fact, that frequency percentages, whether for species or for classes, are largely dependent for their exact magnitude on the sampling method. Comparisons can only be made between communities which have been sampled in a comparable manner. Of course, true frequency of a species exists independently of the effort one extends to ascertain it and consists essentially of the evenness of distribution of the species throughout the community but is quite obviously also related to density. Plant ecologists then must be especially careful to consider what it is they set out to measure and the technique of the problem.

Among the frequency class curves illustrated in figure 8, the one based on the four square meter survey seems to be as similar to the normals as any of the rest. Following Gleason (loc. cit.) we might conclude that the four square meter quadrat size is adequate for sampling this type of woods, at least in so far as the form of the frequency curve is concerned. There is a noticeably strong tendency for the curves to flatten in the middle classes when progressively larger quadrats are used. The significance of this is not apparent to the author at present and is contrary to most results obtained by other workers. Frey (1928) states that the second peak becomes pro-

gressively larger and may surpass the first peak. Class B and C in the twenty-five sq. m. survey are nearly equal (as are D and E); classes B, C, D are nearly equal in the fifty sq. m. survey; in the 100 sq. m. survey all classes are nearly equal except class A.

Rübel (1930, p. 9) emphasizes that frequency data gives the manner of distribution of the species in the stand, and also the spacing between plants of the same species, and the average area of each species in the stand. Lüdi (1928) says that for the determination of frequency small quadrats are used, so large only that the most important species (densest) are found in each quadrat (class E frequency), the remaining species grading off according to their average areas. It thus develops, when rightly taken, that all species in the same frequency class have nearly the same average area. Gleason (1920) has earlier shown that the frequency index of a species is closely related to the number of individuals. "The correlation would be exact if all plants were distributed through the extent of an association precisely in accordance with the laws of probability and chance." This sort of distribution is in fact characteristic of vegetation. Discrepancies which occur are caused in most cases by the dispersal of plants by vegetative means, forming colonies, or in some cases by the recent arrival of a species and the lack of time for it to attain normal distribution. Romell (1930) however has presented evidence that it is not generally possible to translate frequency numbers into density. One factor which seriously interferes is the variable sociability of different species (Braun-Blanquet and Pavillard 1928, and the former 1932).

A recent paper by McGinnies (1934) gives some important information on the relation between frequency and density. On a basis, first, of laboratory tests based on a random sampling of a known number of several different items distributed by chance and, second, an extensive application of comparable methods to natural plant populations, McGinnies concludes that under field conditions, as well as under ideal laboratory conditions, there is a high degree of correlation between frequency index and abundance. He found that, "under both conditions abundance can be calculated for a given frequency index by means of the proper curve or equation," and that the equation proposed by Gleason (1920) is fundamentally sound. Working with two sizes of quadrats he found a high degree of correlation between frequency indices obtained by quadrats of various sizes. It thus becomes possible to adjust the size of the quadrat to the character of the vegetation and the purpose of the investigation. He states that, "There is considerable advantage in the use of a double frame (two sizes of quadrats) for the determination of frequency indices. The two sets of frequency indices serve to some extent as a check on each other: the larger quadrats give a better differentiation of the less abundant species; the smaller quadrats give a better differentiation of the more abundant species; and finally, the frequency indices of the smaller frame, when multiplied by a suitable factor, give an approximation of the abundance of the various species found on the larger quadrats."

Frey (1928) emphasizes that there are essentially two types of species-

distribution curves: 1) those in which the curve drops from left to right, which means that the scarce species are more numerous and the abundant species are fewer; and 2) curves which show two maxims, one for the species which have few individuals and the second for the species with many individuals (the so-called normal curves of Raunkiaer, Kenoyer, Gleason, et al.). Du Rietz asserts that the first type is generally distributed. Scherrer (1923, p. 204) disputes this as in his studies on good characteristic communities of *Molinietum* and *Brometum* he found the first type, while artificially influenced plant communities, as enriched and impoverished meadows (through grazing, manuring, etc.) produce two peaked curves of type two. This difference is probably due to the less variability of ecological factors in the *Molinietum* and *Brometum* and greater variability in the meadows. Romell (1920, cited by Frey 1928) sought to establish the different courses of the curves by theoretical studies. He supports his theoretical curves on the ecological theory that above all the presence or exclusion of this or that species in a plant community (granted, of course, that the species are close enough for migules to enter the community) by the ecological limitations of the community. This has the flavor of Jaccard's proposition that the species richness of a region is directly proportional to the variety of its ecological conditions. Founding his method on the calculation of probabilities of occurrence of 1,000 possible combinations of ecological factors (three factors in ten independent grades of intensity), with an "elementary station" representing the embracing of one such possible combination, Romell obtained both types of curves. If the number of elementary stations is small there prevails a maximum for scarce combinations (for which the probability amounts to less than 20 per cent in the number of stations selected); but when one increases the number of elementary stations there appears gradually a second maximum for the abundant combinations (for which the probability amounts to more than 80 per cent). This would presuppose a species adapted to every ecological combination, with more individuals for the common combinations. This would seem to explain the difference between Scherrer's curves from the more uniform *Molinietum* and the more heterogeneous meadows. Kylin (1926) however, has shown that both types of curves depend on the surface area of the quadrat selected; but he based his theoretical formulation, not on elementary stations, but on "average areas" which is the reciprocal value of the density.

It is worth while to call attention to the relation of frequency class percentages to homogeneity of the plant community. If class E is relatively large the homogeneity of the community is relatively greater. If class A is relatively great the homogeneity of the community is correspondingly less. Such conclusions can be drawn only when stands are compared on a basis of quadrat surveys which are entirely comparable as to size and number of quadrats.

A further interesting point concerns the combination of frequency statistics with constancy statistics (synthesized from several association individuals). Kylin (1926) describes this as a method of obtaining a partial measure of

homogeneity, a sort of average frequency from all association individuals, constancy being something else. Braun-Blanquet (1932) suggests writing it thus 200^{10}, where there are 20 plots in each of 10 stands, and the species is perfect in its frequency. I would suggest its reduction to per cent, for example, 85^{90}, in which the average frequency on 200 plots was 85 per cent and the constancy on 10 stands was 90 per cent; or 85^{100}, if it was present in all stands, etc.

Results of the Second Investigation

About two months after the first six sizes of quadrats were laid out another series was studied. The second series, in August and September, 1932, consisted of twenty-five quadrats each of 1, 2, 3, and 4 sq. m. Previously there had been no three sq. m. plots. Reference to the tables will show remarkable conformity in the data despite the fact that the location of the plots was different, although the manner of distribution was similar. In table 1 it will be seen that the duplicate one square meter plots varied only 0.1 from the average number of species per plot for the first set. The two square meter set varied 0.3, while the four square meter set varied 0.6 from the former averages. These variation are without any statistical significance, i.e. could be due to random sampling, as seen in table 2. At the end of table 6 is found the total number of species in each survey and the average frequency for all species. By comparing these results of the second investigation with those of the first, table 4 it is again seen that there is a remarkable check. The total flora varies only two species for the one square meter size, four species for the two square meter size, and none for the four square meter size. The average frequency of species varies not at all for the one square meter size, one species for the two square meter size and 0.4 for the four square meter size. These results are summarized in table 7. The frequency class percentages, table 8, again show a remarkable check.

Results of the Third Investigation

On working up the data from the 1932 investigations it appeared that quadrat sizes intermediate between the four square meter and the twenty-five square meter plots were desirable. Consequently the woods were revisited in the middle of July, 1933 and two more sets were laid out in the manner of the earlier work. The sizes employed were nine square meters and sixteen square meters. The results are incorporated in the previous tables and in the following table 9. These plots were laid out as follows: the nine square plot was taped out in one corner of the sixteen square meter plot. These plots were spaced equidistant in three rows, the sixteen square meter plots with an intervening space of twenty-six meters each way, the nine square meter plots with a space of twenty-seven meters each way. There were twenty-five quadrats of each size as before.

At first it did not seem that this data supported the results of the former investigations, due to seasonal differences or due to the different location of

the quadrats, as the average number of species fell much lower than the curve indicated. The pitch of the line connecting the nine and the sixteen square meter averages however is not greatly different from that connecting the four and the twenty-five square meter sizes. The main tendency of the curve to flatten still remains at the four meter size. The total number of species from these 1933 surveys is also lower than would have been expected from the curve of the former results. The floristic list from the nine square meter survey is similar to that from the four square meter survey, while the total from the sixteen is close to the twenty-five. These figures would apparently harmonize to produce little change in a smoothed curve. (See figs. 5, 6). Referring to figure 7 we see that the pitch of the line for the average frequency of the species from the nine and the sixteen square meter surveys is almost identical with that of the four to twenty-five segment of the old curve.

The 1933 plots were restricted more closely to the virgin part, about fifteen acres, of the woods formerly investigated. This may have accounted for the smaller number of species encountered and the other variations. The essential point seems to be that the smoothness of the first series was due to the plots being laid in sets concentrated in twenty-five different locations, six to a location, whereas, the later two sets were in entirely different locations. This undoubtedly points towards the necessity for a larger number of plots than twenty-five in a survey of as complex a community as Nash's Woods and not towards the employment of a different size of plot.

TABLE 9

Frequency of species from twenty-five quadrats each of two sizes. Survey of July, 1933.

Floristic list	Frequency per cent: Quadrat sizes 9–m	16–m
TREES		
Acer Negundo L.		4
A. saccharum Marsh.	96	100
Asimina triloba (L.) Dunal	28	32
Carpinus caroliniana Walt.	20	28
Carya cordiformis (Wang.) K. Koch	16	36
C. glabra (Miller) Sweet	28	40
Celtis laevigata Willd.	12	12
C. occidentalis L.		4
Cercis canadensis L.	16	20
Cornus florida L.	44	60
Fraximus americana L.	28	32
F. Bilmoreana Beadle	4	8
F. lanceolata Borck.	40	48
Juglans cinerea L.	4	8
J. nigra L.		4
Liquidambar Styraciflua L.		4
Morus rubra L.	32	32
Nyssa sylvatica Marsh.	36	56
Prunus serotina Ehrh.	20	40
Quercus alba L.	16	16
Q. borealis var. *maxima* (Marsh.) Ashe	32	40
Q. Prinus L.	12	16
Q. rubra L.	4	4
Q. velutina Lam.	4	4
Sassafras officinale Nees & Ebeerm	20	24
Ulmus american L.	4	8
U. fulva Michx.	48	60
SHRUBS		
Ampelopsis cordata Michx.	28	32
Benzoin aestivale (L.) Nees	56	68
Celastrus scandens L.	16	20
Corylus americana Walter	8	8
Evonymus atropurpureus Jacq.	8	16
Menispermum canadense L.	8	20

Floristic list	Frequency per cent: Quadrat sizes 9–m	16–m
Parthenocissus quinquefolia (L.) Planchon	88	96
Rhus Toxicodendron L.	72	72
Sambucus canadensis L.	12	20
Smilax hispida Muhl.	4	4
Symphoricarpos orbiculatus Moench.	8	8
Vitis aestivalis Michx.	12	12
FERNS		
Cystopteris fragilis (L.) Bernh	4	4
Onoclea sensilibils L.	4	4
Thelypteris hexagonoptera (Michx.) Weatherby	12	12
HERBS		
Actaea alba (L.) Mill.	8	8
Agrimonia mollis (T. & G.) Britton	16	36
Apios tuberosa Moench.	16	20
Arisaema Dracontium (L.) Schott.		16
A. triphyllum (L.) Schott.	8	48
Asarum canadense L.	44	44
Campanula americana L.	4	4
Carex pennsylvanica Lam.	52	76
Carex sp?	16	28
Circaea latifolia Hill	48	52
Clematis virginia L.	4	4
Collinsonia canadensis L.	4	4
Cynoglossum virginianum L.		4
Dioscorea villosa L.	16	32
Elephantopus Carolinianus Willd.		4
Galium circaezans Michx.	32	36
G. concinnum T. & G.	12	16
G. triflorum Michx.	8	12
Geranium maculatum L.	12	16
Geum canadense Jacq.	36	68
G. vernum		8
Hackelia virginiana (L.) Johnson	12	24
Hydrastis canadensis L.	4	4
Impatiens biflora Walt.	8	8
Lactuca canadensis L.	4	4
Laportea canadensis (L.) Gaud	28	40
Muhlenbergia sp?	4	16
Osmorhiza Claytoni (Michx.) Clark	8	12
Oxalis cymosa Small		8
Panax quinquefolia L.	4	4
Panicum sp?		8
Phlox divaricata L.	12	20
Pilea pumila (L.) Gray	40	48
Phyrma Leptostachya L.	24	36
Phytolacca decandra L.		4
Poa sylvestris ?	4	4
Polygonum scandens L.		8
P. Virginianum L.	40	60
P. sp.?	8	8
Ranunculus recurvatus Poir.		4
Ruellia carolinensis (Walt.) Steud.	8	8
Solidago caesia L.		4
Silene stellata (L.) Ait.		4
Uvularia grandiflora Smith	4	4
Veronia sp?		4
Viola papilionacea Pursh.	52	64
V. scabriuscula Schwein.	20	20
V. striata Ait.	4	16
Number of species	74	90
Average species frequency	20.8	23.5

NASH'S WOODS AS A FOREST TYPE

The report of the Society of American Foresters (1932) on "Forest Cover Types of the Eastern United States" gives the folowing group of interest to us in a consideration of Nash's Woods:

Central Forest (Fresh to moist)
- Yellow poplar type group
  - Type 53, Yellow poplar
  - Type 54, Yellow poplar-hemlock
  - Type 55, Yellow poplar-white oak-red oak
    - Variant 1, Yellow poplar-white oak-sugar maple
    - Variant 2, Yellow poplar-white oak-black gum-red maple.
    - Variant 3, Yellow poplar-white oak-black oak-mockernut hickory
    - Variant 4, Yellow poplar-white oak.

Type 53 is described as essentially of the Appalachians as a second-growth type, "In small patches yellow poplar still predominates in old growth stands, and the poplar type may once have been extensive in the virgin forest." As to type 54, in Indiana hemlock occurs on radically different sites from yellow poplar, occupying river bluff and canyon walls from Montgomery and Parke counties southeastward. (See, Friesner and Potzger, 1932) Type 55 is also charactertistically Appalachian, although the original forest of the Central States undoubtedly contained more of this type and its variants than the present remnants would indicate—due largely to selective cutting. Variant 1, is described as characteristically developed in middle Kentucky and Tennessee, southward to northern Alabama and eastward to West Virginia. Variant 2 is cited as indicating the wettest site on which yellow poplar naturally grows. Variants 3 and 4 are less closely related to the condition at Nash's Woods.

From a 9.6 per cent strip survey of Nash's Woods we find the following four species of greatest importance, constituting 65 per cent of the total basal area, although but 43 per cent of the number of stems.

	Basal area	*Density, per acre*
Liriodendron Tulipifera	35.9 sq. ft.	12.5 trees
Quercus alba	14.9	5.8
Nyssa sylvatica	15.1	43.3
Acer saccharum	10.5	138.3
23 other species	41.9	266.2
Total, per acre	118.3 sq. ft.	466.1 trees

The following are the most important among the 23 miscellaneous species: *Ulmus fulva, Fraxinus lanceolata, Sassafras variifolium, Liquidamber styraciflua* and *Carya cordiformis,* constituting together 23 per cent of the total basal area and 30 per cent of the total number of stems. It would seem then that Nash's Woods is most closely related to, and intermediate between, variants 1 and 2 of type 55, and can be called a yellow poplar-white oak-sugar maple-black gum variant.

The committee report (loc. cit., p. 2) brings forward again the question of forest type definition (See, Forest Types: Symposium, Soc. Amer. Foresters, 1913) with their usage of the definition established by the Society of American Foresters (1917), with the reservation that "composition" rather than "development" should be the primary basis for recognition of forest types. The definition reads, "A descriptive term used to group stands of similar character as regards *composition* and development due to given physical and biological factors, by which they may be differentiated from other groups of stands. The term suggests repetition of the same character under similar conditions." This brings us to a consideration of Cajander's (1926) admirable summary of the forest type problem, which is too much ignored in this country, and his insistance (loc. cit., p. 20) that, "A natural, uniform, universal and international system. . . . is important from the point of view of forest mensuration and valuation and of forest management generally, of

sylviculture and forest statistics. . ." He comes to a definition (loc. cit., p. 27) very like that of the Americans, "All those stands are referred to the same forest type the vegetation of which, at or near the time of maturity of the stands, and provided the stands are normally stocked, is characterized by a more or less identical floristic composition and by an identical ecological biological nature. . . . Permanent differences call forth a new forest type in cases where they are sufficiently well-marked, or a sub-type in cases where they are less essential, but, nevertheless, noticeable." He goes on, however, to make the point which causes his methods and results to differ fundamentally from ours (loc. cit., p. 31), "All these facts tend to prove that on a basis of forest types it is possible to work out a biological basis of classification of localities essentially independent of species of trees." This is very important where the original natural proportions of the species of trees have been changed by means of man's influences. Thus Cajander comes to a consideration of inferior strata; small trees, shrubs, herbs, mosses and lichens, which are used for purposes of distinguishing site variations within general types as indicated by the tree stratum.

This method would bear patient study in relation to American vegetational problems where many complications in typing are introduced due to the richness of the flora. For example, in the yellow poplar type group we find the Society of American Foresters (1932) listing three types and a number of variants (sub-types, or facies). In this type group a dozen or more species occur besides the yellow poplar (white oak, red oak, black oak, sugar maple, red maple, hemlock, black gum, hickory species, ash species, bass wood, chestnut, magnolia, black birch, black locust, etc.), of which one or more may be associated in varying importance, resulting in a very large number of types which for scientific, if not for practical purposes, must be recognized. Many of these are geographical variants and many are due to the vicissitudes of chance distributions. They do not all represent site differences as certain species are ecologically equivalent over wide edaphic and geographic ranges. In view of the complicated nature of the arborescent stratum it would seem probable that a consideration of the inferior strata might allow a natural biological classification of sites based on the presence or absence of certain species, let us say, for example, dominance by *Cornus florida* and *Carpinus caroliniana* on one site and *Benzoin aestivale* and *Sambucus canadensis* on another site, or *Hepatica acutiloba* and associates on one site and *Impatiens pallida* on another site. The point here is to urge the possibilities of Cajander's system, although the present study on only one woods does not permit its illustration. It does permit emphasis on the value of detailed statistical information concerning the inferior strata.

Nash's Woods and the Association Problem

If we begin our consideration of Nash's Woods as a plant community from Clements' point of view (Weaver and Clements, 1929) we find that it falls better under the Quercus-Castanea Association of the Quercus-Fagus Formation. The authors state that, "Probably no other forest climax in

North America exhibits such a wealth of societies as the deciduous forest," and they go on to mention certain species of small trees, shrubs and herbs making up these strata and aspects. One finds it difficult, however, to be satisfied with so succinct a dismissal of such a far-ranging and variable a complex of communities, even on a basis of the mono-climax theory. For purely practical purposes the foresters find it necessary to recognize many component tree communities and to largely ignore the developmental aspect in favor of that of the contemporary composition. At the same time, however, they find the successional facts of value especially in their development of sylviculture. There is considerably more known to support the poly-climax hypothesis than there is in favor of the mono-climax theory. DuRietz (1930a) in his discussion of "Classification and Nomenclature of Vegetation" before the Cambridge Congress remarked, "Contrary to the mono-climax theory developed by Clements and Braun-Blanquet, I find it necessary to maintain the poly-climax theory developed by Domin, Gams, Gleason, Nichols, Nordhagen, Scharfetter, Tansley, myself, etc. (compare, DuRietz 1930b), i.e. to admit that several climax-phytocoenoses, in many cases with very little relationship to each other—may occur side by side in the same vegetation-region, but in edaphically different habitats (edaphic climax of Nichols). My own field experience certainly does not support the theory of the power of a uniform climate to transform all these edaphically different habitats into one comparatively uniform *climax-habitat, climax-soil,* etc., as postulated by the mono-climax theory."

Gleason (1926, p. 9) has well remarked that "our various theories on the fundamental nature, definition, and classification of associations extend largely beyond the bounds of experiment and observation and represent merely abstract extrapolations of the ecologist's mind," but it applies less truly to certain European methods and systems than to ours. Gleason (loc. cit., p. 11) emphasizes that what is generally recognized as one and the same association (for example, *Pinus Strobus* forest) does not have precisely the same environment in different areas. However, Gleason himself would no doubt readily recognize that the floristic composition of the inferior strata on various white pine sites would permit a distinction among these various white pine forest types as well as site types. One might suggest as a possibility a *Pinus Strobus-Taxus baccata*-association, a *Pinus Strobus-Viburnum alnifolium*-association, a *Pinus Strobus-Oxalis acetosella-Clintonia borealis-association,* etc. As to the reverse, that apparently identical environments may be occupied by entirely different associations, one can readily admit, with the reservation that different species groups, however they may have originiated on equivalent sites, frequently result in ultimate environmental differentiation—as that of increased soil acidity due to evergreen undergrowth. Also, the fact that "local variation in structure merges gradually into the broader geographical variation of the association-type" does not deter the plant sociologist from attempting to systematize the ultimate distinctions he finds in the field. All these difficulties to the contrary notwithstanding, we can not agree with Gleason (loc. cit., p. 15) that, "Surely our belief in the

integrity of the association and the sanctity of the association-concept must be severely shaken." The continued activity of plant sociologists over the world stands as testimony to the fact and need. Granting the fundamental thesis of the individualistic concept of the plant association, that it is the visible expression, through juxtaposition of individuals, of the primary causes, migration and environmental selection, we find, not that every plant community is essentially different (nor that there is any precise identity), but that, nevertheless, over wide areas there will develop readily recognized "association individuals" of an "association." These association individuals (stands), of course, show variation from one to another, as all biological phenomena must, but their essential similarity makes them recognizable as a "kind" of plant community. Local differences, changes in percentage composition of widespread species, or the presence or absence of certain species, makes for the recognition of sub-associations, or facies. Gleason's argument (loc. cit., p. 23), "The sole conclusion we can draw from all the foregoing considerations is that the vegetation of an area is merely the resultant of two factors, the fluctuating and fortuitous immigration of plants and an equally fluctuating and variable environment," contains a fatal omission, that of the influence of the "dynamic behaviour" of certain species (Braun-Blanquet et Pavillard, 1928) which are "constructive," "conserving," and "consolidating." Granted an heterogeneous community in a given environmental situation, due to fortuitous immigration (yet with the limitations of the flora of the region), the competition and reactions of these species will in many similar, if not identical sites, in time result in the dominance of one or more of a certain group of species in the various strata. As a result, here and there over thousands of square miles, thousands of acres come to support similar vegetational complexes, so similar, in fact, that one has little difficulty in typing them, to wit, 97 forest types in Eastern United States (Soc. Amer. Foresters, 1932), each of which "must actually be found occupying in the aggregate hundreds of thousands of acres." (loc. cit., p. 3.)

As Nichols (1929) has pointed out in his discussion and criticism of Gleason's individualistic concept of the plant association, "It should be borne in mind that in attempting to classify the facts of nature, we are dealing with merging phenomena." Gleason himself has worked with many plant associations in the field and would certainly hold no objection to any plant sociologist's description and definition of an *association individual* based on statistics of the stand, or of an *association* based on empirical data synthesized from statistics of several association individuals. One can only conclude that his lack of faith is not so much in actual association, which he admits exist, but in theoretical "associations" and "various theories on the fundamental nature, definition, and classification of associations (which) extend largely beyond the bounds of experiment and observation. . . and (which) suffer from the vagaries and errors of human reason."

Däniker (1928), who has advanced arguments for an ecological basis for the division of plant communities has made a good distinction in separating, "*Pre-communities*, in which the individuals are not regulated through mutual

effects" from "*True communities* with mutual determination of the organization of the individual (plant community) through the habitat influence and therewith a tendency towards an individual balance (equalization or uniformity)." Within the latter Däniker recognizes: 1) pioneer communities with minimal active habitat influences; 2) communities with distinct habitat influence by single pioneer communities and 3) communities with very strong habitat influences through the peculiar habitat divisions, and therefore far-reaching differentiation and stratification appears. The strata are in turn organized like communities. Especially the ruling stratum in individual uniformity corresponds to type 2 above. This point of view serves to emphasize the role of the component species in determining the nature of the plant community and is further argument against Gleason's individualistic concept.

The problem of the association becomes progressively more complicated in the several-layered communities, as Nash's Woods. DuRietz (1930a) in his discussion of "Classification and Nomenclature of Vegetation" before the Cambridge botanical congress remarks that, "While the lowest units of phytocoenoses (see, Gams, 1918), the sociations, are founded upon a relative homogeneity in all layers, most consociations are homogeneous only in one layer, and the higher units in no layer at all, being founded mainly upon the sociological affinity of the dominants of the layer arbitrarily chosen as base for the classification (mostly the highest one of the layers represented). Thus most phytocoenoses of higher rank than the sociation are natural units only in one layer, each of the other layers consisting of alternating synusia (Gams, loc. cit.) with very little relationship to each other." As Rübel (1925, and 1930, p. 25) remarks in his discussion of synusia, "Not all plants of an association fit under the same ecology, it gives as a result, ecological groups (synusia) within an association. . . . In the ecological description of an association one must group these synusia. They correspond in many instances with the strata, however, not always, as, for example, in tree-trunk-epiphyte communities."

If we are able to take Lüdi's statement (1928) that, "The fundamental unit of sociology is the association as the species is the fundamental unit of systematics" and Flahault and Schröter's well-chosen definition of the Brussels botanical congress, "Eine Assoziation ist eine Pflanzengesellschaft von bestimmter floristischer Zusammensetzung, einheitlichen Standortsbedingungen und einheitlicher Physiognomie," we immediately encounter difficulties in dealing with the several-layered community complexes. It seems to the author that Lippmaa (1933) has come forward with a valuable and far-reaching suggestion based on several years of intensive field work: that, "*The associations are to be defined as one-layered plant communities*" (einschichtige Pflanzenvereine). Layer societies, synusia, etc. have long been recognized as bearing somewhat loose relations to their superior strata and to frequently occur with essential similarity as layers or synusia under totally different superior strata, for example, a Cornus-Carpinus-Ostrya understory to beech-maple in one stand and to yellow poplar-white oak in another stand.

At first it seems unreasonable to consider several associations to be grow-

ing simultaneously on the same terrain. Lippmaa (1933) elucidates his thesis by comparing a several-layered woodland with a hochmoor, which latter is in reality an equally natural vegetational unit as a woods, but which is readily and justly subdivided into horizontal associations (and in the hochmoor there exist essential differences in height of the communities). Why is it not equally justifiable to consider the layers as separate associations, for do not the hochmoor associations frequently extend under one another, in part at least? It could be emphasized that the woodland layers are dependent on one another, and to a certain extent that is true, but more often the dependence is on the general protection and environmental modification afforded by the superior stratum than it is on any floristic nature of the stratum. As Lippmaa emphasizes for the *Hepatica triloba-Pulmonaria*-association, it is dependent on the forest humus and shade but largely independent of the floristic nature of the arborescent stratum. He thinks the hypothetical several-layered associations which we find described in the literature have to be given up for two reasons: 1) The appearance of an extraordinary abundance of single associations that belong to a certain natural complex; 2) The extraordinary heterogeneity of a many-layered "association" considered from the standpoint of life-forms. The number of species constituting an association (a single-layered association) does not effect their validity, that depends on the floristic richness of the region and the number of species which chance to be ecologically equivalent in the flora of the region. Lippmaa's point of view is entirely new and seems to offer a way out of several of our classificatory problems. It serves again to emphasize the necessity for careful and detailed statistical analyses based on natural vegetational groups.

One might conclude the argument by suggesting that Nash's Woods consists of the following associations: 1) *Liriodendron Tulipifera-Quercus alba-Acer saccharum-Nyssa sylvatica*-association, 2) *Cornus florida-Carpinus caroliniana-Cercis canadensis*-association, 3) *Benzoin aestivale-Sambucus canadensis*-association, 4) *Rhus Toxicodendron-Parthenocissus quinquefolia*-association, 5) *Viola-Arisaema*-association, which are probably duplicated elsewhere in the same relationship;—but the complex will be found in many places with one or another of the layers missing, with additional layers, or with one or more other associations in the place of the ones named.

Such names as these for the associations should, however, be taken tentatively until the specific nature of the general dominants is established by wide comparative studies. There is probably little question about the validity of associations 1, 2 and 4. Associations 3 and 5 are more variable and have less well-marked dominants.

Potzger and Friesner (1934) writing on the composition of Mauntel's Woods (section A), a virgin forest patch in DuBois County, Indiana, note that *Rhus Toxicodendron* is the most frequent species of the ground cover, frequently of almost complete coverage. They also state that the woods is "unique on account of the absence of the common second layer trees, i.e. *Carpinus caroliniana* and *Ostrya virginiana*. . . The only second layer tree which was present in any worthwhile representation was *Cornus florida*. The

woods is of the Quercus-Carya-association group. Cain (1932) on Donaldson's Woods, a virgin white oak tract in Lawrence County, Indiana, found that *Cornus florida* especially, and *Ostrya virginiana, Carpinus caroliniana, Cercis canadensis* and *Sassafras variifolium* compose the inferior tree stratum. *Parthenocissus quinquefolia* and *Rhus Toxicodendron* were also highly represented in the ground cover. Unpublished quadrat studies by the author on Dillon's Woods, DuBois County, Indiana, reveal similar conditions to those of Nash's Woods. In an almost pure woods of *Fagus grandifolia* (with an understory of *Acer saccharum*) in Parke County, Indiana, Esten (1932) found *Parthenocissus quinquefolia* and *Evonymus obovatus* of especial importance in the ground cover, and Cornus, Carpinus, and Ostrya forming the second layer. Cain in an unpublished quadrat study of Warren's Woods, Berrien County, Michigan, a virgin beech-maple tract, found Cornus, Carpinus, and Ostrya again of importance in the inferior tree stratum; *Benzoin aestivale* and *Vibrunum acerifolium* in the shrub layer; *Parthenocissus* and *Rhus Toxicodendron* on the floor. Quick (1923) found Ostrya important in the beech-maple climax of Southern Michigan. Bergman (1923) reports Ostrya and Carpinus as playing their usual roles in the maple-basswood climax communities of Minnesota, as also Parthenocissus.

As such statistical studies accumulate (on old aged, and mostly virgin forest tracts) one becomes impressed with the independence of certain layer communities of their superior strata, and the general validity and utility of Lippmaa's concept. As illustrated above the Cornus-Carpinus-Ostrya-Cercis group, which occurs with essential integrity under several forest types, as white oak, oak-hickory, poplar-oak, beech, beech-maple, maple-basswood, etc., seems to be an association in its own right, dependent on an overstory of larger trees, but independent of their floristic composition, within certain limits. As a consequence one might reasonably expect that a field study of this particular problem would enable the establishment of such an one-layered association of small trees (understory trees) with definite geographical facies, and likewise for other one-layered associations.

Conclusions

1. Data were obtained on the influence of quadrat area on the quantitative results of investigations utilizing quadrats in groups of twenty-five for each survey (for each quadrat size). These data were treated mathematically and they uniformly point to the four square meter quadrat size so far as it seems possible to indicate which of the quadrat sizes used constitutes the minimum area necessary for adequate sampling. The indication of this minimum quadrat size arises from:

a) The average number of species per quadrat;
b) The total floristic list from each survey;
c) The average frequency for all species of a survey;
d) The similarity to Raunkiaer's frequency class curve.

The data from a, b, and c were plotted against area to form parabolic and

saturation curves. The point at which these curves flatten most strongly was taken to be an indication of the minimum adequate quadrat area (for the number of quadrats used).

2. A method of computing frequency ratios for species and total surveys was found to be useless for determination of minimum quadrat area.

3. Since these various methods of analysis all point to the same minimum quadrat area it would follow that any one method would be sufficient for the purpose of determining the minimum quadrat area. As one of the species-area curves would be most easily obtained, its use is suggested for this purpose.

4. It is obvious that workers in vegetational problems of the quantitative analytical type would find it desirable to know the minimum quadrat area that they could use with satisfactory results. An area too small would give inadequate data; an area too large would increase the labor without increasing correspondingly the accuracy of the results. Furthermore, it is highly desirable to maintain a constant sample area size for studies on comparable plant communities, for only on such a basis can the results be compared.

5. This data is especially inadequate in two respects:

a) The vegetation was not analysed separately for each stratum, i.e. a separate minimum quadrat area should be found for each vegetational stratum;

b) No study was made of the effect of increasing the quadrat number, say to 50, 100 or more quadrats.

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A NOTABLE CASE OF BOG FORMATION*

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A great many papers have been written on bogs and bog vegetation, but little or nothing has been said of a young developing bog, one which is in the active process of forming. No doubt such cases are rare. In this respect, then, Baxter's Bog in Monroe county, Indiana is a unique place. It is isolated from large bog areas and vegetatively has passed from the tree stage to high shrub stage within the lifetime of the older settlers in the county. A few species of plants present are at least 150 miles out of their reported range for the state.

Much misunderstanding exists over the real meaning of the terms "swamp" and "bog." Tarr and Martin (1920) say, "A swamp is a part of the surface of the land which is wet and saturated with moisture though not usually covered with water. Some swamps are called marshes, bogs, muskegs." Some botanists differentiate between the two on the basis of their formation, i. e. a swamp filling from the bottom up and a bog filling from top and bottom both. Other workers differentiate on the basis of acidity of the soil, still others on the basis of xeromorphic structure of the plants dominant in such places. None of the definitions given holds true in every case, for there are areas which are truly bogs, formed by the growth of Sphagnum on surfaces without depressions; acidity of soil, too, is not adequate as a line of differentiation, for there are bogs which are not acid and low wet lands with acid soil which no one would classify as bogs.

The writer is of the opinion that classification is best made on the basis of the nature of the soil, and in this respect agrees with Kurz (1928), "Peat is part and parcel of bogs," and with Rigg (1916), "They are formations of the surface of the earth which have been formed by plants and which always have at the surface a mass of decomposition products rich in carbon which consists of pure plant substances." European workers almost universally differentiate between bogs and swamps on the nature of the substratum. Just to quote a few of these: Thienemann (1925) says, "In a moor the accumulated plant remains form a dense tough peat." Hayek (1926), too, recognizes peat as the outstanding feature of a bog, the water table being at or near the surface level of the soil, while in swamps peat is absent, and the water table is above the surface of the soil, which soil may be rich in humus. Harnisch (1929) gave as his definition the one formulated by Ruester (Die Subalpinen Moore des Riesengebirgs Kammes): "A moor is a continuous

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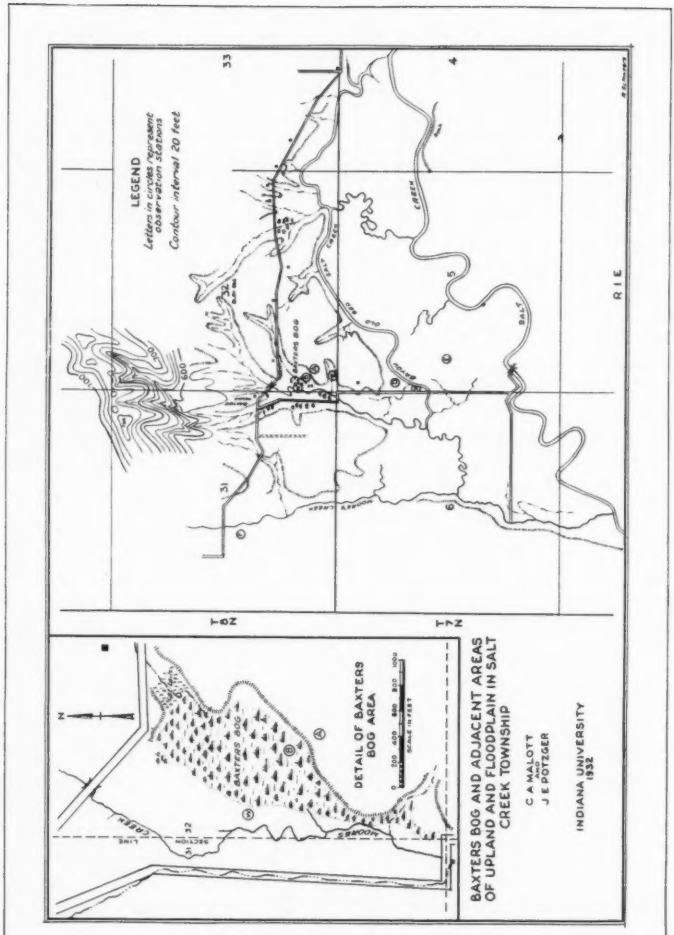
LEGEND
Letters in circles represent observation stations
Contour interval 20 feet
BAXTERS BOG AND ADJACENT AREAS OF UPLAND AND FLOODPLAIN IN SALT CREEK TOWNSHIP
C A MALLOTT
J E POTZGER
INDIANA UNIVERSITY
1932
DETAIL OF BAXTERS BOG AREA
SCALE IN FEET
BAXTERS BOG
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Fig. 1.

surface area of the topography whose moisture-loving vegetation, under influence of surface and ground water, causes a mass accumulation of decomposition products rich in carbon (living moor), or has accumulated (dead Moor)."

The author discusses this conception in detail, saying, "Such a definition embraces a double meaning. It characterizes the moor as a geological conception, for it precludes the formation of a definite soil type, peat, but also includes a specific biological condition which functions in the formation, a formation which occurs in situ by the activity of a specific plant community. In other words, it characterizes a moor as a life association (biome) which causes the formation of a specific type of soil."

It seems well, then, to define a bog as a feature of the topography where the water table is at or near the surface and the soil is of organic origin (peat) formed in situ. Swamps, on the other hand, are features of the topography where the water table is above the surface and the soil is chiefly inorganic or of a humous nature. Basing the differentiation between bog and swamp on the nature of the substratum will classify as bogs the filled-in depression areas, acid or alkaline in reaction, as well as the bog in Monroe county, Indiana, which is in the formative period, still devoid of plants with xeromorphic structure.

Fig. 1.

Much of the original land surface of the United States consisted of areas of retarded drainage which the Department of Agriculture lists as swamp and overflow land. In their report of 1908, Document 443 (1909), they gave an estimate of the amount of such land still remaining in the various states. Indiana was credited with an acreage of 625,000 acres, of which 15,000 acres were permanently swampy land. Most of these swamp and bog areas are in the northern counties. These more extensive areas are undoubtedly due to continental glaciation. The most common form of bog formation is the filling in of small lakes; but a good many bogs are also formed in other depression areas and along river courses. If an area of retarded drainage is within a humid region where rainfall is in excess of evaporation, swamps and bogs are certain to develop. Indiana is located within such a region, and so we find wet lands along most of the river courses. In case thte smaller streams must traverse a wide flat valley before reaching the master stream, part of the sediment will be deposited where the gradient becomes low, fallen trees may further retard drainage, a pool develops behind such an obstruction, debris continues to accumulate, and if the soil is impervious, and water-retaining vegetation such as Sphagnum develops, the swamp may eventually become a typical bog. An example of such a developing bog is found in Baxter's Bog, located in Salt Creek township, Monroe county, Indiana. (Fig. 1)

Physiography of Baxter's Bog*

The most important stream in Monroe county is Salt Creek. It is an old glacial sluiceway, rising in the northwestern part of Brown county and emptying into White river southwest of Bedford in Lawrence county. It

Fig. 2. Eroding Pleistocene river terraces.

must have been a powerful stream in the past since its valley is a half to a mile wide. Its course is tortuous, the river bed is excavated to a depth of fully twenty-five feet in the old alluvial plain. In some places of the flood plain are vast deposits of Pleistocene river terraces composed of clay mixed with quartzite pebbles. All along its course in Monroe county are intermittent swampy areas where little tributary streams descend from the steep uplands heavily loaded with sediment, and deposit this as they reach the wide flat alluvial plain. Baxters Bog is one of these wet lowlands, located on a tract

* The title is used for the first time. It was selected in honor of James O. Baxter, one of the first pioneer settlers in the township. His log cabin was located near the bog.

of land owned by the Bloomington Basket Factory. Sphagnum has invaded the place, and it is now in the early stages of bog formation, typical bog species are just coming in. It is at the junction of two small streams about eighty rods from the upland within the high old river terraces, about three-quarters of a mile from Salt Creek. (Fig. 1)

During high water, the streams are heavily charged with mud washed from the old terraces (Fig. 2), but now depositing this mostly before the bog is reached. No doubt Salt Creek was at one time swinging close to the northern border of its valley. This may readily be inferred from the presence of old bayous (Fig. 1), remains of old cut-offs and meanders. Numerous bayous filled with water only at flood time, give evidence of gradual shifting to its present position. As the plain was being filled, the smaller streams coming as tributaries were much impeded by the low gradient of the flood plain and swamp land developed. The small streams have in time aggraded the land along their course, filling in between their banks, thus the smaller stream which forms the bog area was gradually ponded by the aggradation of the larger stream along the outlet of the smaller one (Fig. 3). This natural levee ponded the water where the young bog is now located to approximately seven feet at the maximum depth.

In addition to the normal rainfall and stream-water accumulation, seepage from the old river terraces enters at several places like springs. This water kept up a steady flow even during the dry summer of 1930.

Floristic Aspect of the Bog

As stated previously, Baxters Bog is in the initial stage of sphagnum-bog formation. In the former lowland woods stage it was evidently dominated by the sub-climax species of the region, i. e. *Quercus palustris* and *Quercus bicolor*, with probably some representation of *Acer rubrum*, of which but a few relics remain, with very little reproduction of these species occurring. Even within the knowledge of the older settlers, Baxters Bog supported forest made up of the species just mentioned, but after they had been cut no young growth developed. The present dominant species in the bog are the high shrubs *Ilex verticillata* and *Alnus rugosa*.

The bog is still rapidly expanding in surface area. The higher levee strips between the streams flanking the bog are dominated by *Fagus grandifolia*, old trees, fully two hundred years of age as ring counts showed, and these trees are gradually being crowded out by the expanding bog (Fig. 4). *Alnus rugosa, Cephalanthus occidentalis*, Salix spp. make up the border vegetation with occasional patches of *Solidago patula* and *Rosa palustris* coming in. The deeper more shaded part of the bog is covered with a luxuriant growth of Sphagnum, about the only place within a radius of seventy-five miles where this moss is found. The expansion of the bog is also evidenced by the migration of the moss. Along the eastern border of the bog is one of the old river terraces heavily timbered with Fagus, Carya, Liriodendron, rising sharply from the edge of the bog. The Sphagnum is

advancing from the bog proper out on the slopes along decaying logs, probably also aided in this advance by socies of *Polytrichum commune*, Leucobryum, and Dicranum.

The few typical bog species which have made their appearance indicate that Baxters Bog is still in the early stages of development. However, it must be remembered that migration of such species to the area is made difficult by the distance which separates the habitat from similar areas of

Fig. 3. Filled in lower edge of Baxter's Bog, x marks mouth of little stream which carries seepage from the bog.

more mature development. The bog species which have come in are: *Ilex verticillata* (L.) Gray; *Decodon verticillatus* (L.) Ell.: *Aspidium cristatum* (L.) Sw.: Sphagnum sp.; *Habenaria clavellata* (Mx.) Spreng.; *Bartonia virginica* (L.) BSP. The latter two have been reported for Indiana only from northern counties up to this time.

The higher bank rim is occupied almost exclusively by *Fagus grandifolia*, with a second layer of *Carpinus caroliniana*, and a shrub layer of *Asimia triloba*. Fagus dominates at present wherever the land is elevated above the water table from six to ten inches and more. The critical point seems to be near the creek, for as soon as the land slopes towards the bog, Fagus disappears. The only trees present in the bog are *Quercus palustris* and *Acer rubrum*. However, these two species must be relics of a former vegetation since very little young growth is found. The shrubs Ilex and Alnus form the dominant layer at the present time. Ilex is limited to the bog exclusively.

This feature of the vegetation is shown in figure five, representing an area of five by ten meters. Ilex was represented with 197 stems and Alnus with sixty stems. Both Ilex and Alnus grow in dense clumps, their crowns make an unbroken canopy under which Sphagnum, *Aspidium cristatum,* and

Fig. 4. Row of dead Fagus marking rim of extending bog area.

Osmunda cinnamomea grow most luxuriantly. There are no stretches of open water but numerous places where the soil is very dilute and soft. In the open places where the shrubs do not shade, one finds *Decodon verticillatus* and *Solidago patula* (Fig. 5).

The present vegetation points to a gradually developing bog in which the trees are relics of a past climax, now being displaced by shrubs. This is also indicated by the dying Fagus consociation along the outer rim, the encroachment of Alnus, and the presence of *Scirpus grayphyllus* Vahl., *Polygonum arifolium.* The prolific growth of Sphagnum is steadily adding to the moisture of the bog.

Sphagnum as Bog-Former

Of all plants, Sphagnum is probably the most important bog-former. It can endure a very wet habitat admirably; it grows rapidly in dense mats to form what Shaler (1890) calls a thick sheet of vegetation." It needs no undersoil, the entangled shoots form sponge-like meshes which are capable of retaining a vast amount of water. "The particles of water are so enclosed by the filaments of the plants that evaporation takes place slowly and the water is readily drawn up from below by capillarity." Needham and Lloyd (1930). These authors continue to say that the most characteristic single organism in such habitats is Sphagnum. The growth of the moss is cushion-like, the stems are unbranched and soft which can retain an upright position only through the support which comes from mass. This moss makes up the greater part of the ground cover at Baxters Bog (Fig. 6).

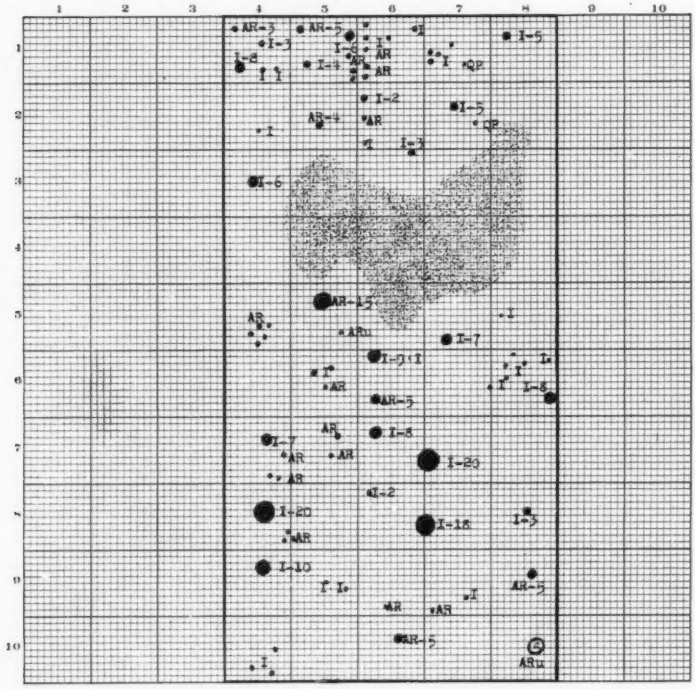

Fig. 5. Project, Station "B" Alnus-Ilex Associes. Quadrat No., 5 x 10 Meters in Bog Habitat. October 18, 1931. Location, Salt Creek Township. Mapped by Potzger.

AR—Alnus rugosa; ARu—Acer rubrum; I—Ilex verticillata; QP—Quercus palustris; Figures—Stems in a clump; Shaded area—Solidago patula socies.

Fig. 6. Typical section of dense Sphagnum growth clustering about the base of shrubs and trees.

TABLE 1

Summarized quantitative data on pH investigation at Baxter's Bog

Soil	Depth of soil	No. of samples	pH range	Average active acidity	Av. active acidity in pH
Seepage from terrace		6	5.61-6.38	13.96	5.87
Peat soil	Surface	3	4.62-5.08	116.76	4.93
Peat soil	One foot	5	4.81-6.29	42.82	5.38
Peat soil	Two feet	5	5.11-6.4	20.91	5.68
Peat soil	Three feet	5	5.27-6.46	14.2	5.85
Peat soil	Four feet	5	5.46-6.45	12.1	5.92
Peat soil	Five feet	5	5.67-6.31	8.9	6.06
Peat soil	Six feet	5	5.80-6.31	7.6	6.12
Base of Sphagnum		8	5.10-6.4	33.83	5.48
Terrace	Surface	5	4.62-6.43	57.83	5.23
Terrace	3-inch	5	4.71-5.18	134.08	4.88
Terrace	12-inch	6	4.49-5.27	176.3	4.76

The young bog, thus, by nature of the described vegetation retains very uniform soil moisture which is not noticeably changed by either rainfall or continued drought. The Sphagnum grows more luxuriantly in this Monroe county bog than in any bog the writer has ever visited, even in the northern Michigan region. The whole area is well shaded by the tall shrubs and this aids in the reduction of evaporation (based on actual measurements with atmometers) to half of that in the mesophytic Fagus consociation but fifty feet distant on the river terrace. (Fig. 1A)

SOIL ACIDITY

Acidity of soil is among the numerous edaphic factors which are considered as having a more or less modifying influence on the establishment of plants in a habitat. According to Bushnell (1926), all the soils of eastern Monroe county are acid. This was substantiated by 218 samples taken in the various habitats of the Salt Creek township area. Determination was for active acidity (pH) of the soil; measurements being made with the Youden Hydrogen-ion Concentration apparatus, an electrical method.

It was a surprise to find the bog soil less acid than that of the adjacent upland terraces (Fig. 1, A, B). The peat soil was tested at every foot of depth to the six foot level, and it showed a uniform progressive decrease in active acidity from the surface to the six foot level (Table 1). The soil at the base of Sphagnum plants showed less active acidity than either the surface or one foot peat soil (Table 1). Kurz (1928) found a definite correlation between high acidity and proximity to Sphagnum, his work showed a lateral and horizontal decrease in acidity away from Sphagnum. In the present investigation we do not find such a correlation. There is a vertical

decrease in active acidity, but the acidity is less at the base of Sphagnum than a distance from the plant or even at the one foot level of the peat. Sphagnum bog soil in this case is even less acid than the soil on the old river terraces. The present findings, thus, do not agree with Kurz (1928), who says; "It follows that mosses cause much of the local acidity," for soil about both Sphagnum and upland mosses and lichen showed less active acidity than most of the upland and flood plain soils. There is no doubt, that a bog habitat as a unit will be invaded by typical bog species, which is indicated by the invasion of such species as *Habenaria clavellata* and *Bartonia virginica* in Baxters Bog, but it must be because of a complex of edaphic factors of which acidity of soil is evidently but one.

Discussion

Baxters Bog is an unusual area, not only is it singularly isolated in a region without typical bogs, but it also has a unique history of development. The northern bogs develop most commonly from hydrophytic beginning successionally through stages of filling and accumulation, here at the Monroe county bog the process is reversed, by regression and gradual expansion of wet soil the forest was eliminated and shrub dominance was initiated, and this within the time of the present generation of men. Since the initiation of the bog formation, peat has accumulated to a depth of six feet at the maximum depth. While northern bogs decrease in extent of wet habitat, this bog is increasing in this respect. The forest is in the last struggle for dominance, typical bog species have just invaded.

The area is also interesting from the standpoint of succession and plant migration. Whence came Sphagnum, Habenaria, and Bartonia of which the latter two had their former reported range at least 150 miles to the north? The migration to the area by typical bog species has been and will be slow due to the isolated position of the bog. The floral representatives of bog species in this bog substantiate the opinion expressed by Gleason (1923), "Migration of a species depends on an environmental change within or beyond its range. . . . numerous other considerations offer convincing evidence of the nature of the process such as the relation of the associations to physiographic development, the reaction of the plant cover on the environment."

Physiographically the place is ready for a bog vegetation, its isolation will make invasion slow, for the plants' individual modes of dispersal will be inadequate for the distance to be spanned between the present habitat and the area in Monroe county. If one considers succession from hydrophytic and xerophytic habitats to mesophytic climax as progressive succession, here, then, we have a most striking case of regressive succession; for the physiographic development is regressive, hence, the phenomenon of migration is emphasized so much more by the appearance of species which are typically suited to the habitat.

If we consider the bog species as relics, we must assume that bog areas similar to Baxters Bog had existed in Salt Creek valley and have been

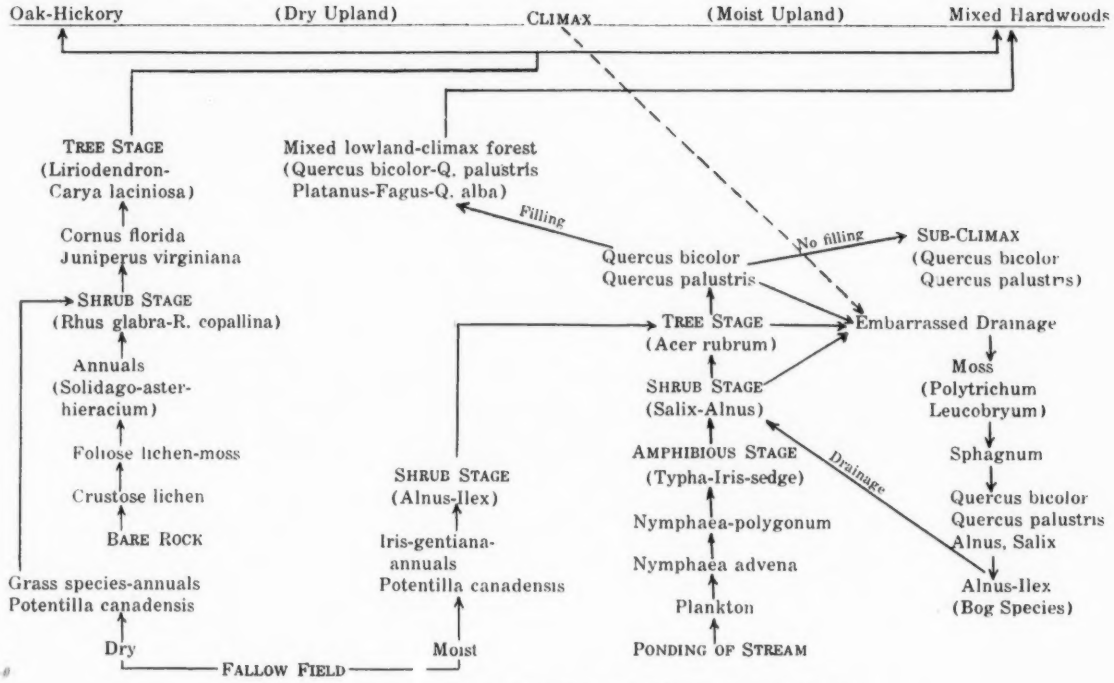

Fig. 7. Plant Succession in Salt Creek Township, Monroe County, Indiana

destroyed either by alluviation or through the activity of civilized man, and all traces of their existence have been lost. On the other hand, if we consider their presence as invasion, dispersal must have been accomplished by birds. The typical successions in Salt Creek township in Monroe county are shown in figure eight.

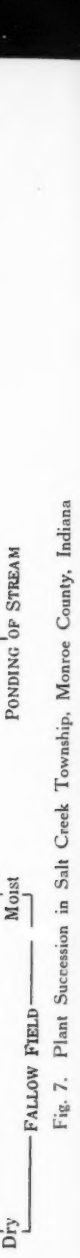

Fig. 7. Plant Succession in Salt Creek Township, Monroe County, Indiana

Summary and Conclusions

1. Differentiation between bog and swamp has been made on the basis of the nature of the substratum.
2. Baxters Bog is a typical area of regressive succession, shrubs superseding trees.
3. The bog is in a youthful stage of formation.
4. Typical bog species are represented by Sphagnum sp., *Ilex verticillata Decodon verticillatus, Bartonia virginica, Habenaria clavellata.*
5. Habenaria and Bartonia have previously not been reported for Indiana except from the far northern counties, about 150 miles distant from Monroe county.
6. *Alnus rugosa* and *Ilex verticillata* are dominant in the present vegetation of the bog.
7. Six feet of peat have accumulated at the maximum depth.
8. Active acidity decreases progressively downward with each foot of depth of peat soil.
9. Sphagnum does not show an acidifying influence on the soil immediately surrounding it.

Acknowledgements

The writer is gratefully indebted to Dr. D. M. Mottier for suggestion of the field of research, as well as for numerous helpful thoughts while the work was in progress; to Dr. Stanley A. Cain for valuable suggestions, critical reading of the manuscript, and photograph of the bog; to Dr. C. A. Malott for the time spent to do the major part of the mapping of the region; to the officials of the Bloomington Basket Factory for granting permission that the work might be carried out on their property; to Mr. Wm. Baxter for valuable information on the forest of the Salt Creek township region.

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PROF. SHEPARD'S TREES OF GREENE COUNTY

BENJAMIN FRANKLIN BUSH

It has just been brought to my attention that in *The Plants of Greene County, Missouri,* by Prof. Shepard, no species of tree is mentioned. It would seem that this was more than a mere coincidence, and suggests that Prof. Shepard must have prepared the list in this manner. This supposition is supported by the discovery of a list of trees of Greene County published by Prof. Shepard in the Geological Survey of Missouri for the year 1898, volume xii. This report deals chiefly with several areas in Missouri, and with Greene County in particular, with much information on the rocks, lime, minerals, springs, water, etc., and on pages 46 and 47 there is a list of trees. We are interested in this list, the exact title of which is "A List of the Native Trees of the (Greene) County," by Prof. E. M. Shepard, President of Drury College, Springfield, Missouri.

In this list there are 78 names of trees and shrubs; and as I feel that very few people have ever seen it, I am presenting it now just as it was published. Nearly half of the names in this list seem to me worthy of comment, and I have made corrections and notes as I now understand the species. The only change I have made in this list is in the numbering of the species. Otherwise it is presented just as Shepard published it with his names and his arrangement.

For reference as to the names and ranges of species, I have used the admirable "Trees in Kansas," by Dr. F. C. Gates, of Manhattan, Kansas, which is almost indispensable to the student of trees in Western Missouri, Oklahoma, and Kansas.

1. *Juniperus virginiana* L. No doubt about this species, but in Tracy's *Flora* some years before, Shepard reports this as *J. communis.*
2. *Juglans cinerea* L.
3. *Juglans nigra* L.
4. *Hicoria alba* (L.) Britton.
5. *Hicoria glabra* (Mill.) Britton. Certainly not this species, which is an eastern form, but which may possibly occur in the sand hills in Dunklin County. However, two species of Hicoria that Shepard does not mention, *H. arkansana* and *H. ovalis,* are common in Southern Missouri; and I suspect Shepard must have had one or the other and misidentified it as *H. glabra.*
6. *Hicoria laciniosa* (Michx. f.) Sargent.
7. *Hicoria microcarpa* (Nutt.) Britton. Probably what is known as *H. ovalis,* a species not recognized at the time Shepard prepared his list, but which is common in the Ozark region of Missouri.

8. *Hicoria minima* (Marsh.) Britton.
9. *Hicoria ovata* (Mill.) Britton.
10. *Populus monilifera* Ait.
11. *Populus tremuloides* Michx. Certainly not native in Greene County. I have never seen this species in cultivation anywhere. Nurserymen often call *P. alba* "aspen" and "American aspen," and I suspect Shepard must have mistaken this for *P. tremuloides*.
12. *Salix humilis* Marsh. This is merely a shrub, never attaining the height of a tree.
13. *Salix nigra* Wardii Bebb. Usually a low, bushy shrub, rarely becoming a small tree. The Black Willow, so abundant along the larger streams, is not mentioned by Shepard, although it must occur in Greene County.
14. *Ostrya virginica* Willd.
15. *Corylus americanus* Walt. The Hazlenut could scarcely be termed a tree by anyone.
16. *Quercus alba* L.
17. *Quercus imbricaria* Michx.
18. *Quercus minor* (Marsh.) Sargent.
19. *Quercus macrocarpa* Michx.
20. *Quercus Muhlenbergii* Engelm.
21. *Quercus nigra* L.
22. *Quercus palustris* DuRoi.
23. *Quercus prinoides* Willd. As usually found this is only a scrubby shrub two or three feet tall, rarely up to twenty feet.
24. *Quercus rubra* L.
25. *Quercus texana* Buckley. Certainly not the Texas Red Oak. I assume that the tree Shepard found was *Q. Schneckii*, a species he does not mention in his list, which is the common red oak of Southern Missouri.
26. *Quercus velutina* Lam.
27. *Ulmus alata* Michx. As usually found in the Ozark Region, this is only a bushy shrub, attaining the size of a tree farther south, at much lower altitudes along streams.
28. *Ulmus americana* L.
29. *Ulmus pubescens* Walt.
30. *Celtis occidentalis* L. Not the eastern tree, which does not occur in Missouri, but no doubt either *C. canina* or *C. crassifolia*, two species Shepard does not mention in his list. Another species, *C. laevigata*, must also occur in Greene County.
31. *Morus rubra* L.
32. *Toxylon pomiferum* Raf. Commonly planted in the State for hedges, windbreaks, etc., but certainly not native in Greene County. Many years

ago I found many large old trees of this species along the Cowskin River in McDonald County; and as there were no hedge fences in that County, the trees appeared to be native in that place.

33. *Liriodendron Tulipifera* L. I cannot imagine what species of tree Shepard found common along the Sac, as this tree does not occur in Missouri anywhere near Greene County; but I suspect that he must have mistaken *Nyssa sylvatica* for it, as he does not include it in his list.
34. *Asimina triloba* (L.) Dunal.
35. *Sassafras Sassafras* (L.) Karst.
36. *Benzoin Benzoin* (L.) Coulter. Could scarcely be considered a tree in any sense of the word by anyone.
37. *Liquidamber Styraciflua* L. Certainly not native in Greene County, and seldom or never seen in cultivation.
38. *Platanus occidentalis* L.
39. *Pyrus coronaria* L. Not the *P. coronaria* of the Southeastern States, but probably *P. ioensis Palmeri* or *P. lancifolia.*
40. *Pyrus ioensis* (Wood) Carruth. Perhaps correct, but might be the variety *Palmeri* or the variety *Bushii,* both of which are more or less common in the Ozark Region.
41. *Amelanchier canadensis* L. Probably this species, as this is the only species we have in Southern Missouri; but Shepard lists this as *A. oblongifolia* in Tracy's *Flora.*
42. *Crataegus coccinea* L. The scarlet haw does not occur in Missouri, and it is probable that some species of the *molles* group was found and identified as *C. coccinea.*
43. *Crataegus tomentosa* L. Not the real *C. tomentosa* of the Eastern States, but probably some species of the *tomentosae* group.
44. *Crataegus Crus-galli* L. The true *C. Crus-galli* probably does not occur in Greene County, but no doubt some species of the *Crus-galli* group was found by Shepard.
45. *Prunus americana* Marsh. Certainly not the eastern *P. americana,* which is merely *P. nigra* and is confined to the seacoast of the Eastern States. May be some form of what is now known as *P. Munsoniana* or *P. lanata.*
46. *Prunus angustifolia* Marsh. Possibly this species, which is scarcely ever a tree, but more likely some form of *P. Munsoniana* or *P. lanata.*
47. *Prunus hortulana* Bailey. Possibly this species, but more likely some form of *P. Munsoniana* or *P. lanata.*
48. *Prunus serotina* Ehrhart.
49. *Prunus virginiana* L. Very improbable that Shepard found this species in Greene County, as it ranges more northerly in Missouri.
50. *Cercis canadensis* L.
51. *Gleditschia triacanthos* L.
52. *Robinia pseudacacia* L. Certainly not native in Greene County, but com-

monly planted in the State for ornament and windbreaks. Many years ago I found along the bluffs and cliffs of the Cowskin River in McDonald County many old trees, whose size and age seem to attest the fact of their being native in that locality.

53. *Xanthoxylon americanum* Mill.

54. *Rhus copallina* L.

55. *Ptelea trifoliata* L. The real *P. trifoliata* does not reach Greene County, and it can scarcely be said to be a tree. No doubt Shepard found some species of Ptelea, of which there are several shrubby species in Southern Missouri, and took it to be *P. trifoliata.*

56. *Rhus glabra* L. This can scarcely be considered a tree, as it is commonly less than eight feet high.

57. *Rhus hirta* (L.) Sudw. Certainly not the R. *hirta* of the Eastern States, as that has not been found in Missouri. Shepard has this in Tracy's *Flora* as *R. venenata,* another species not known for Missouri.

58. *Euonymus atropurpureus* Jacq. This can scarcely be called a tree, as it does not attain the height of one.

59. *Staphylea trifolia* L. This also must be considered only a low, bushy shrub or at most a tall shrub.

60. *Acer Negundo* L. Not the eastern *A. Negundo,* which only reaches our State in the southeastern part, but no doubt one or another of several other species of *Negundo* known to occur in Missouri.

61. *Acer rubrum* L. Certainly not this species, as it occurs only in the southeastern part of the State, unless it should be that the trees were cultivated.

62. *Acer saccharinum* L.

63. *Acer saccharum* Marsh. Not the tree of the Eastern States, and either *A. subglaucum* or *A. Rugelii,* as these are common in parts of Missouri.

64. *Aesculus glabra* Willd. Very doubtful, as it occurs only along the Missouri River and Mississippi River valleys. Very likely it must be one of several species known to occur in Southern Missouri.

65. *Rhamnus lanceolata* Pursh. This is considered a mere shrub.

66. *Tilia americana* L. Although common in the Missouri River region, this species is not definitely known from the Ozark region; and it is probable that some one of several species known to occur in Southern Missouri was collected by Shepard.

67. *Cornus Amomum* Mill. This is a mere shrub with no claims whatever to the title of tree.

68. *Cornus candidissima* Marsh. This is merely a shrub; but I suspect Shepard must have found *C. asperifolia,* an abundant species in most parts of Missouri, and determined it as *C. candidissima,* as he does not mention *C. asperifolia* in his list.

69. *Cornus florida* L.

70. *Diospyros virginiana* L.

71. *Fraxinus americana* L.
72. *Fraxinus lanceolata* Borck.
73. *Fraxinus quadrangulata* Michx.
74. *Catalpa Catalpa* (L.) Karst. This species, with several Asiatic species, is in cultivation throughout the State; but it is not native to Missouri.
75. *Cephalanthus occidentalis* L. This species is merely a shrub.
76. *Sambucus canadensis* L. Never considered a tree by anyone, but a bushy, much-branched shrub.
77. *Viburnum Lentago* L. This species, so far as I know, has not been found in Missouri, although quite lately Mr. Kellogg writes me that he has found it in St. Louis County. I am assuming that Shepard must have found some form of *V. prunifolium* and mistook it for *V. Lentago*.
78. *Viburnum prunifolium* L. Possibly this species, but more likely *V. rufidulum*, a species not given by Shepard in his list, and which is the prevailing form in Southern Missouri.

COURTNEY, MISSOURI.

STUDIES ON CESTODA OF POULTRY FOUND IN AND AROUND DOUGLAS COUNTY, KANSAS*

Q. B. FERRY

Introduction

The purpose of this investigation** is to determine what species of tapeworm infest the domestic chicken, *Gallus domesticus,* in and around Douglas County, Kansas, and the extent of the infestation. This work was started in the Fall of 1932 and was continued until the early Spring of the following year.

The fifty domestic chickens for this investigation were procured from the Central Produce Company, in Lawrence, Douglas County, Kansas, with the kind help of Mr. Lewis Goodrich, a former classmate to whom I wish to express my gratitude for his assistance.

The chickens were delivered to the poultry house by different farmers in Douglas County, and were intended for food consumption by the people of Lawrence.

I found six species of cestodes, three of which belong to the genus *Raillietina;* one to the genus *Amoebotaenia;* one to the genus *Choanotaenia;* and one to the genus *Hymenolepis.* Although all of these species have been previously described, I have found some new and interesting morphological peculiarities which either differ from those previously described, or have been overlooked entirely. Therefore, a discussion of these forms is warranted.

This work has been done upon the suggestion and under the direction of Miss Mary E. Larson, Assistant Professor of Zoölogy, to whom I wish to express my appreciation for her interest and valuable criticism.

I also wish to extend my thanks to Dr. James E. Ackert, Professor of Zoölogy, Kansas State College of Agriculture and Applied Science, for his valuable suggestions and help in identifying some of my specimens.

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* Presented before the Kansas Academy of Science Meetings, April 14-15, 1933, at Manhattan, Kansas, U. S. A.

** Contribution from Zoölogical Laboratory, University of Kansas.

Literature

The problem of cestode infections in domestic fowl, *Gallus domesticus*, has received a great deal of attention in the United States for the last few years. The North American helminth faunas have been worked out by such prominent investigators, as Stiles (1896), Ransom (1900), Guberlet (1916), and Ackert (1919).

There are five important species of cestodes known to infest domestic chickens, (Guberlet, 1916, 218), *Choanotaenia infundibuliformis, Hymenolepis carioca, Raillietina cesticillus, R. echinobothrida,* and *R. tetragona.* This is corroborated by Ackert (1917), who also found two common parasitic nematodes, *Ascaridia lineata* and *Heterakis papillosa,* occurring frequently in domestic chickens of all continents.

In the old world, Grassi and Rovelli, (1889, 1892) have shown that the intermediate host of *Davainea proglottina* is a slug, *Limax cinereus.* Ransom (1909, 68) recorded the presence of *Davainea proglottina* in Pennsylvania and Maryland. This is the first record of this parasite within the United States. Guberlet (1916) states, however, that this species has not been reported in this country. Evidently Guberlet overlooked the report of Ransom in 1909, hence it has led to the general belief that this species has never been introducd from Europe. Ransom, however, failed to give any discussion in his publication except the citation in a footnote. The first observation on the life history of *Davainea proglottina* in the United States was undertaken by Chandler in Texas in 1923. He successfully experimented with the slug, *Agriolimax agrestis,* which is one of the species that Grassi and Rovelli were successful in infecting, and found that it serves as an intermediate host in the United States as well as in Europe. The occurrence, therefore, of this species in Pennsylvania and Maryland, and in Texas as determined by Chandler (1923, 144), indicates as rather wide distribution in the United States.

The chicken cestodes are found usually in the small intestines. Eleven species of tapeworms have been reported by Stiles (1896, 10), from the domestic chicken, *Gallus domesticus,* and sixteen species by Ransom (1909).

The mode of transmission of fowl cestodes has been experimentally demonstrated by Grassi and Rovelli (1892) by finding body larvae whose scolices closely resembled those of *Choanotaenia infundibuliformis* Goeze in the common house fly, *Musca domestica* Linn. Guberlet, (1916, 235), succeeded both in infecting *Musca domestica* with cysticerci by feeding onchospheres of this tapeworm, and in rearing adult worms by giving house flies to fowls. Ackert (1918, 41) reared *Raillietina cesticillus* (Molin) in domestic chicken by feeding with *Musca domestica.* Piana (1881-1882) found that the larval stage of *Monocercus Davainea tetragonae* developed in the snails, *Helix carthusianella* or *H. maculosa.* Ackert (1919, 34) succeeded in transferring the infection from one fowl to another by feeding the experimental chicks with the common house fly infected with *Raillietina tetragona.* Up to the present time there is no record of investigations of the transmission of *Raillietina echinobothrida* to fowls. Some authors have expressed doubt as to whether *Raillietina tetragona* and *R. echinobothrida* represent two distinct species. Von

Linstow (1872b, 56-67) discovered *Amoebotaenia sphenoides* in chickens in Germany, and described it as *Taenia cuneata*. Piana (1882, 393-4) examined similar tapeworms but failed to add much information to the diagnosis. Grassi and Rovelli (1889a, 404, 1892, 29-30, 88-90) found the same species in Italy. They observed some cysticercoids in an earthworm, *Allolobophora foetida* Eisen, which they believed represented the larval stage of *T. cuneata*. They did not undertake any experiment to determine this point, although they assume that the hooks agree with those of *T. cuneata*. This intermediate host must therefore be subjected to experimentation before Grassi and Rovelli's statements are fully accepted. Magalhaes (1892, 145-6) reported the same species from Brazil, and added several important details on the morphological structures of the tapeworm. Railliet (1892, 53) used the specific name *Taenia sphenoides* for this cestode on the ground that *Taenia cuneata* was already preoccupied. In 1893 Railliet reverted this form to *Dicronotaenia cuneata*, and three years later, he put it under the *Dicronotaenia sphenoides*. Cohn (1901b) fully described this species under the erroneous name *Amoebotaenia cuneata*. *Taenia cuneata* von Linstow 1872 is a homonym of *Taenia cuneata* Batsch 1786; hence, Ransom modified the name to *Amoebotaenia sphenoides*. Under the International Code of Zoölogical Nomenclature the name *cuneata* can not be employed for the species described by von Linstow in any generic combination. Meggitt (1914) reported the presence of *Amoebotaenia sphenoides* in chickens in England, and described its anatomical structures. He experimented with the earthworm, *Allolobophora foetida* Eisen as a medium of transmission to chickens, but failed to substantiate the claim of Grassi and Rovelli. Meggitt (1931, 254) reported also for the first time from *Anseriformes* in Burma. Tubangui (1926) reported this species of cestode from the domestic chickens in the Philippines. Ransom reported this species from Maryland and the District of Columbia in 1909. Just before this paper was ready for publication a report by Adams and Geiser (1933, 253) from Dallas County, Texas, shows that 8% of the poultry that were examined in 1927 were infected with *Amoebotaenia sphenoides*. These are the only records for this parasite in the United States which I have been able to find However, Guberlet's (1916, 218) neglect of Ransom's paper led to the general belief that this species has never been observed in North America.

The dwarf thread-like cestode, *Hymenolepis carioca* Magalhaes, may be transmitted by the stable fly, *Stomoxys calcitrans* according to Guberlet (1919, 237), who succeeded experimentally in rearing the adult tapeworms in young chickens fed upon stable flies from poultry yards.

Method of Procedure

The duodenum, small intestine proper, large intestine or rectum, and the two blind intestines, commonly known as ceca, were placed in small glass containers for me by Mr. Goodrich or his assistants. He noted the weights and sexes of the fowls before dressing. In many instances, I was present to take down the necessary data. The examination of the intestines was made as soon as possible after the material was obtained from the poultry house. Unless noted otherwise, the parasites were examined alive.

The intestinal tract, from the duodenum to the anus was straightened out by snipping the mesenteries, then slit open and freed from obvious helminths. The open gut was cut into pieces, almost a foot in length, and soaked in luke-warm water. I found that it is possible to leave the worms in the warm water for some time without apparent injury. The visible cestodes were placed in physiological salt solution for binocular examination. Finally, the supernatant was poured off, the sediment was examined over a black surface, and the remaining visible helminths were picked out with a hooked needle or fine brush. From two to four decantations were employed, and the débris examined for further parasites present.

Fixation

The helminths after binocular examination were placed in 10 per cent formalin solution for one hour (Wardle, 1932, 244), and then removed to 5 per cent formalin solution. I tried other fixatives, but formalin is preferable for my materials. I used Bouin's solution and found it to be good for cestode preparation, but it requires a longer time and consumes more alcohol than any other fixative.

The cestodes are removed from 5 per cent formalin and washed in running tap water over night. They were then placed between the two slides and suffiicient pressure was applied to flattem them out and make them as thin as possible. They were stained in a dilute Hematein, C. P. for from 12 to 24 hours according to the thickness of the specimen, then washed in tap water for 1 to 5 minutes and dipped in Eosin B. for 2 to 5 minutes. The specimens were washed well in several changes of tap water, passed through 30 to 70 per cent alcohol for 5 to 10 minutes each, and finally destained with acid alcohol (50 c.c. of 70% alcohol plus 6 drops of HC1). After sufficient destaining they were immersed in alkaline alcohol (50 c.c. of 70% alcohol plus 6 drops of .1% aqueous solution of bicarbonate of soda) until the blue color was restored, and then removed to 95 per cent alcohol for 10 to 30 minutes. Thereafter, the slides were transferred to absolute alcohol for 10 to 40 minutes and then placed in the Oil of Wintergreen until cleared (6 to 12 hours). The slides were separated and balsam added to the slide on which the worm was left. A cover-slip finished the permanent mount.

Discussion

Morphological Structures

Family *Hymenolepididae* Railliet & Henry, 1909

Subfamily *Dipylidiinae* Stiles, 1896

Genus *Amoebotaenia*, Cohn, 1899

Amoebotaenia sphenoides (Railliet, 1892) Cohn, 1899

Diagnosis: Body 2 mm. (von Linstow) to 3 mm. (Magalhaes) long, by 1 mm. broad, wedge-shaped; scolex 180 μ wide by 240 μ long, contracted posteriorly to form the neck (Stiles). My specimens showed prominent neck with 124 μ long by 212 μ broad; neck absent according to Cohn, (1901b);

retractile rostellum, cylindrical, 75 μ in length by 52 μ in width, bearing 10-14 hooks, dorsal root 19 μ long and ventral root 28 μ long. Suckers round to oval, unarmed. Segments 14-22, increasing gradually in size from the first to the last, so that the entire body is wedge-shaped. Genital pores irregularly alternate (Stiles) or regularly alternate, situated almost at the anterior corner of the segments; male organs appear in first segment. Testes spherical from 10-12 in number, lying in a single row on the dorsal surface of the posterior end of the proglottid. Vas deferens coils and serves as seminal vesicle. Ovary bilobed on ventral surface of the segment. Receptaculum seminis present. Uterus persistent. Vagina differentiated from the posterior surface of the cirrus. Average number of mature proglottid eleven, and mature eggs in the last three or four segments, the last of which shows the eggs rather densely scattered than the preceding gravids. Width of last mature segment 816 μ by 145 μ in length, while the gravid proglottid 1073 μ wide by 24 μ long. Eggs spherical with two protecting membranes, outer covering 25 μ in diameter, inner membrane 22 μ. Onchospheres 19 μ in diameter and its visible hooks from 4 to 6 in number.

The tapeworms are thin and very fragile, and therefore, difficult to handle and stain. They localize in the duodenum and are attached to its wall.

Two female chickens were found to be parasitzed with *Amoebotaenia sphenoides*. Rare species of castodes such as *Davainea proglottina* and *A. sphenoides* were found only in certain localized regions such as Maryland, Pennsylvania, the District of Columbia, and Texas. My findings of *Amoebotaenia sphenoides* confirm the introduction of this species of cestodes in this country.

Genus *Choanotaenia* Railliet, 1896

*Choanotaenia infundibuliformis** (Goeze, 1782) Railliet, 1896

Diagnosis: Length 2 to 9 mm. or 50 to 200 mm. (Guberlet, 1916, 24). Scolex small rounded about 400 μ in diameter. Rostellum armed with a single row of 16 to 20 hooks, 25 to 30 μ long with long dorsal root and short ventral root. Suckers round to oval, 175 μ in diameter. Neck short about 125 μ long. Anterior proglottid very short, 17 to 40 μ in length, and as they become older funnel-shaped, much narrower at the anterior than at posterior margins; posterior segments 250 μ long by 450 μ wide. Genital pores irregularly alternating, situated one in each segment in the anterior third of the lateral margin, usually under cover of the backward projecting border of the preceding segment. Vas deferens and vagina pass between excretory canals, and dorsal to nerve trunk.

Of all the chickens examined only a male has been found to be infected with *Choanotaenia infundibuliformis*. This species is the most active cestode observed. The two specimens of this species measure from 2 to 17 mm. long. The smaller was the more active. It moved by protruding its scolex with the rhythmic contraction of the first proglottid followed by the succeeding segments.

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*According to the law of priority the correct name of this species is *Choanotaenia infundibulum* (Bloch, 1779).

Genus *Hymenolepis* Weinland, 1858

Hymenolepis carioca (Magalhaes, 1898) Ransom, 1902

Diagnosis: Length 25 to 65 mm. or 30 to 80 (Guberlet, 1916, 39). Neck 70 to 150 μ broad, at posterior end 500 to 700 μ. Segments from three to five times or more broader than long throughout trobila. Head flattened dorso-ventrally. Suckers shallow, 70 to 90 μ in diameter, unarmed (Guberlet). Rostellum unarmed; in retracted position 25 to 40 μ in width and 90 to 100 μ in length, with small pocket opening to exterior in anterior position. My specimens show the suckers as well as the rostellum very faintly. Unsegmented neck portion of strobila 500 to 1500 μ long. Genital pores almost entirely unilateral, a single pore being located in each segment slightly in front of middle or right-hand margin.

There was an equal distribution of parasitism caused by *Hymenolepis carioca,* ten males and ten females harboring this tapeworm. These parasites were very numerous in two of the chickens examined. In the case of the first, I ceased counting when I had recorded 500, and from the second I removed more than 200. *Hymenolepis carioca* Magalhaes is thread-like, and usually occurs in great number. It is very delicate and fragile, and can be recognized by these factors alone.

Family *Davaineidae* Fuhrmann, 1907

Subfamily *Davaineinae,* Braun, 1900

Genus *Raillietina,* Fuhrmann

Raillietina cesticillus (Molin, 1858) Blanchard, 1891

Diagnosis: Length 7 to 65 mm.; 9 to 45 mm. (Molin); 100 to 130 mm. (others). Head globular or flat, 320 μ long by 460 μ broad; rostellum convex or spherical, not prominent, 330 μ broad, armed with about 210 hooks 7 to 8.5 long, arranged in double rows; these hooks have a very dorsal and a long ventral root; suckers not prominent. Neck absent. Strobilation of the worm becomes aparent immediately behind the head, and very distinct within a distance o ftwo millimeters. Anterior segments from 3 to 5 times as broad as long, being broader than the head, but very short; the following segments increasing gradually in size; borders overlapping. Genital pores irregularly alternate. Eggs elliptical 70 to 80 μ, hooks of onchosphere 16 to 17 μ, or 18 to 23 μ (Dujardin).

Of the thirty-one chickens infected with *Raillietina cesticillus,* sixteen were males and fifteen females. This cestode is the most common in this region.

Raillietina echinobothrida (Mégnin, 1881) Blanchard, 1891

Diagnosis: Length 50 to 100 mm. by 1 to 4 mm. broad, Stiles, 1896, 49) up to 250 mm. long. Scolex small, cuboid, its summit presenting an infundibulum armed with about 100 hooks, 7 μ long, and with 200 hooks, (Guberlet), arranged in a double row. Suckers large, armed with several circular rows of hooks, the hooks of the middle row are the largest; with age these

hooks fall and the suckers gradually become indistinct. Neck present. Anterior segments very thin, 50 times broader than thick; following segments increasing gradually in size, posterior border overlapping, so that the margin of the strobila appears serrate. Eggs spherical 70-90 μ in diameter, arranged in groups of 6-8 in roundish egg capsules.

Two guts of male chickens were dissected and found to be parasitized with *Raillietina echinobothrida*.

Raillietina tetragona (Molin, 1858) Blanchard, 1891

Diagnosis: Length 12 to 90 mm. (Molin), or 190 mm. by 1.5 to 3 mm. broad. Scolex small, tetragonal; retractile rostellum armed with about 100-200 hooks, 5-7 μ long. Suckers round to oval, armed with seven or eight concentric rows of hooks of varying size. Neck very long. Anterior segments very short; the following sub-quadrangular, the posterior edges overlapping. Genital pores unilateral or irregularly alternate, situated in or about the middle of the margin. Eggs arranged irregularly in groups of 10-25 in egg capsules.

Nineteen birds, ten males and nine females, were found infested with *Raillietina tetragona*.

Conclusion

Sixty-two per cent of the fowls were infested with *Raillietina cesticillus*. The number per fowl was fairly constant, except in two extreme cases in which one had 235 worms, and the other had 334.

Three species of cestodes, *Amoebotaenia sphenoides*, *Choanotaenia infundibuliformis*, and *Raillietina echinobothrida* appear to be uncommon parasites of domestic chickens of this region. The first was found in 4 per cent of the fowls, the second in 2 per cent, and the third in 4 per cent.

Thirty-eight per cent of the chickens were parasitized by *Raillietina tetragona*.

The thread-like tapeworm, *Hymenolepis carioca*, which infested 40 per cent of the chickens, and *Amoebotaenia sphenoides*, were localized in the duodenum.

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LAWRENCE, KANSAS.

All drawings except figure 7 are drawn at the same magnification with the aid of a camera lucida, and then reduced one-half.

Spencer microscope No. 79533
L. P. lens No. 42239 — 16 mm N. A. 0.25.
H. P. lens No. 41371 — 4 mm N. AP. 0.75.

Micrometer
L. P. — 8.33 μ equal to 1 space.
H. P. — 1.72 μ equal to 1 space.

Camera lucida
L. P. — x110
H. P. — x500

PLATE XXI

Amoebotaenia sphenoides.

Fig. 1. Whole tapeworm.
Fig. 2. Sexually mature proglottid.
Fig. 3. Transverse section of mature proglottid.
Fig. 4. Gravid proglottid.
Fig. 5. Rostellar hooks.
Fig. 6. Scolex with few segments showing distinctly the neck region.
Fig. 7. Embryos drawn at H. P. with the aid of a camera lucida, and then enlarged -x2.

PLATE XXII

Choanotaenia infundibuliformis

Fig. 8. Scolex well extended.
Fig. 9. Entire worm showing rostellum with rostellar sac and hooks.
Fig. 10. Sexually mature proglottid.
Fig. 11. Gravid proglottid.

Hymenolepis carioca

Fig. 12. Scolex showing rostellum and suckers unarmed.
Fig. 13. Sexually mature proglottids.
Fig. 14. Gravid proglottids.

PLATE XXIII

Raillietina cesticillus

Fig. 15. Scolex showing rostellar hooks.
Fig. 16. Sexually mature proglottid.
Fig. 17. Gravid proglottid.

Raillietina echinobothrida

Fig. 18. Scolex showing suckers and rostellum armed with hooks.
Fig. 19. Sexually mature proglottid.
Fig. 20. Gravid proglottid.

Raillietina tetragona

Fig. 21. Scolex showing suckers and rostellum armed with hooks.
Fig. 22. Sexually mature proglottid.
Fig. 23. Gravid proglottid.

PLATE XXI

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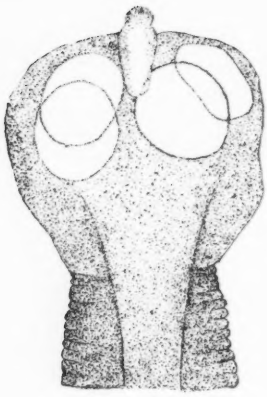
PLATE XXII



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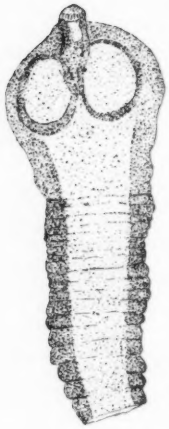

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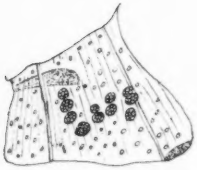

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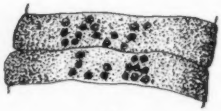

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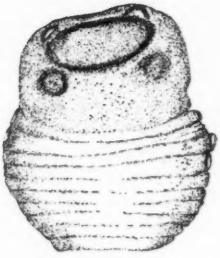
PLATE XXIII



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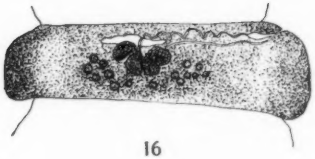

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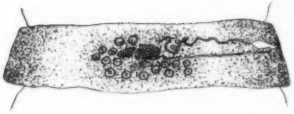

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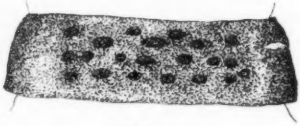

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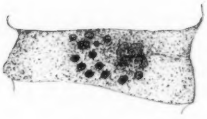

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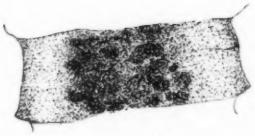


23

THE DISTRIBUTION OF THE DOWNY WOODPECKER (DRYOBATES PUBESCENS) IN EASTERN KANSAS

W. S. LONG

The Southern Downy Woodpecker, *Dryobates pubescens pubescens,* was first taken in Kansas by Wetmore, at Independence, Montgomery County, January 3, 1905, but he did not report it until 1915. At this time he suggested that the birds had followed the valley of the Verdegris River north into the southern part of the state.

Isely (1912) reported that *Dryobates pubescens pubescens* is the common form found at Wichita, Kansas. However, he did not give any measurements in proof of his identification.

In the summer of 1915, Vic Housholder and a party of students collected a number of Downy Woodpeckers from Cherokee, Labette and Montgomery counties, for the Kansas University Museum. These were classified as *Dryobates pubescens medianus.*

In an attempt to determine the exact status of these two subspecies, the writer measured all of the skins in the collection of the Museum of Birds and Mammals. He also collected specimens in some of the counties from which no skins were available.

According to Ridgway (1914) the subspecies of the Downy Woodpecker are differentiated chiefly on the basis of size, which is best expressed in terms of wing measurement. The dividing line has been set at 91 mm., the southern race ranging from 86.5 to 91, and the northern form from 91 to 97.

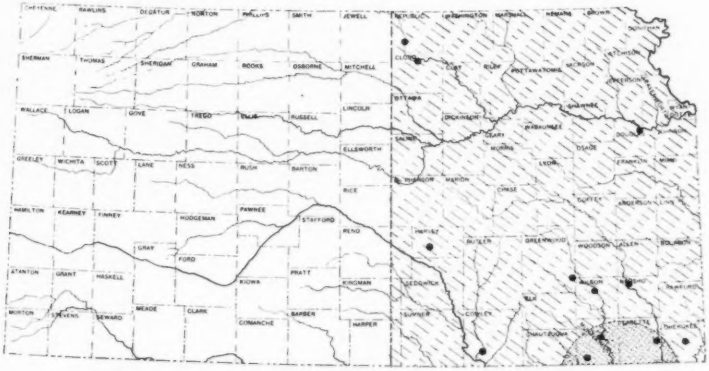
A study of the wing measurements of more than two hundred and fifty skins from Kansas, shows that, on the whole, the Downy Woodpeckers of the state are intermediate between *Dryobates pubescens pubescens* and *Dryobates pubescens medianus.* In Montgomery and Labette counties, which are traversed by the Verdegris and Neosho rivers, respectively, the majority of the birds are referable to the southern race. Eleven skins from these two counties average 89.5 mm., and only one is larger (92) than Ridgway's maximum for *D.p. pubescens.* A larger series from these counties would undoubtedly show many specimens with wing measurements in excess of 91, but the facts seem to support the theory that the southern race has pushed up the Verdegris River into southern Kansas.

In order to determine whether or not the same condition exists along the Arkansas River in southern Kansas, the writer collected five specimens in Cowley County, near Winfield. This is only a few miles from the Arkansas River, and about fifteen miles north of the Oklahoma line. These specimens are referable to *D.p. medianus,* and the birds of the Wichita area, about thirty-five miles to the northwest, are undoubtedly of this same form, instead of the southern race, as reported by Isely (1912).

This conclusion is further supported by Nice (1931) who reports *D.p.*

medianus from central Oklahoma, almost directly south of Winfield, Kansas. She also reports the southern form nesting at Copan, just a few miles south of Caney, Montgomery County, Kansas, where Housholder and his party collected *D.p. pubescens*. It is probable that *D.p. pubescens* does not go farther north than the southern row of counties, since six specimens from Neosho and Wilson counties prove to be *D.p. medianus*, averaging almost 94 mm.

Eight skins from Cherokee County also prove to be *D. p. medianus*, although this county is as far south as Labette, and adjoins it on the east. Doctor Wetmore has suggested that this may be due to the influence of the Ozark highlands of Southwestern Missouri.



Dashes indicate range of *Dryobates pubescens medianus*.
Dots indicate range of *Dryobates pubescens pubescens*.
Spots indicate localities from which specimens were examined.

LIST OF SPECIMENS EXAMINED

All measurements are in millimeters

County	No. of spec.	Minimum	Maximum	Mean
Cloud	7	91	96	93.3
Republic	7	91	93.5	91.9
Douglas	209	88	97.5	92.6
Harvey	7	90	95	93
Greenwood	4	89	95	92
Neosho	3	92	95	93
Cowley	5	90	95	92
Wilson	3	93.7	96.5	94.7
Cherokee	8	88.5	96	92
Labette	5	87	92	89.6
Montgomery	6	88	90.5	89.4

MIGRATION

Migration among the Downy Woodpeckers is probably very limited. If a short migration were universal, the summer specimens should be referable

to the southern form, and winter birds should be of the northern race, but this is not the case. Doctor Wetmore's two specimens of *D. p. pubescens* were taken in the winter and early spring. Many winter specimens from Douglas County have typical wing measurements of the southern race.

Mr. W. B. Bell, of the Bureau of Biological Survey, has kindly furnished me with the banding records of Downy Woodpeckers. These show little movement from the place where the subjects were banded. Out of five hundred returns, there is evidence of migratory movement in only two cases. A bird banded on January 15, 1927, at Canton, Missouri, was shot on July 5, 1927, at Burlington, Iowa, only fifty or sixty miles north of the banding place. Another one banded on February 2, 1925, at Elkader, Iowa, was found dead at Balsam Lake, Wisconsin, about 175 miles north, on October 25, 1925. This indicates that only occasional individuals migrate, and that their migrations are not very extensive. It is very probable that the Downy Woodpeckers of southeastern Kansas are practically resident.

The writer is indebted to Doctor A. Wetmore for helpful suggestions and criticism; to Mr. C. D. Bunker for permission to use the material in the collection of the Museum of Birds and Mammals; to Doctor H. H. Lane, of the Department of Zoology, University of Kansas, who has been of much help in the study, and to Mr. W. B. Bell, of the Bureau of Biological Survey, who kindly furnished the banding records, concerning Downy Woodpeckers, of that organization.

Summary

1. The Downy Woodpeckers of Eastern Kansas are intermediate in size between *Dryobates pubescens pubescens* and *Dryobates pubescens medianus*.
2. *Dryobates pubescens pubescens* pushes up the Verdegris and Neosho rivers into Montgomery and Labette counties, southeastern Kansas.
3. Birds from Cherokee County, in the southeastern corner of Kansas, are of the northern race, probably as a result of the influence of the Ozark highlands of southwestern Missouri.
4. *Dryobates pubescens pubescens* does not occur along the Arkansas river in southern Kansas.
5. There is little migratory movement among the Downy Woodpeckers of Kansas, since specimens of the southern form have been taken both in winter and summer.

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EPISTOMINOIDES AND COLEITES, NEW GENERA OF FORAMINIFERA

HELEN JEANNE PLUMMER

Two rather rare species of foraminifera diagnostic of Midway strata in Texas until recently have been represented by too few specimens to permit a full and accurate understanding of their structure. In 1927, when the Midway foraminiferal fauna was described* one of these was unfortunately designated *Pulvinulina reticulosa* Plummer n. sp. from a single and apparently perfect specimen that has since proved to possess a terminal aperture obscured by extraneous matter. The other has recently been designated *Saracenaria wilcoxensis* Cushman and Ponton from an outcrop of fossiliferous Wilcox marl where the form is exceedingly rare and from which material has probably seen insufficient for adequate description of its structure.

Fortunately an outcrop of the Mexia clay member of the Wills Point formation of the Midway group** has now been found where both *"Pulvinulina" reticulosa* Plummer and *"Saracenaria" wilcoxensis* Cushman and Ponton occur in sufficient numbers and in an excellent state of preservation, so that material is now adequate to elucidate all the architectural details of the tests, which are referred now to the two new genera, *Coleites* and *Epistominoides*. The description of this new exposure is as follows:

Steep bank along the east side of a tributary flowing due north into Tehuacana Creek, about 2 miles in a direct line north and slightly west of the center of the town of Mexia, about one-quarter of a mile west of the railroad, Limestone County, Texas. The very compact, grey, fossiliferous clay carrying numerous small corals lies within the Mexia clay member of the Wills Point formation and about 35 feet above the top of the Tehuacana limestone. These clays are very rich in exquisitely preserved foraminifera, ostracods, and other shells, and for the study of the genotypes of the genera *Coleites* and *Epistominoides* this locality is much better than the type localities for the species. A few yards north and west of this outcrop and along the same creek lignitic Wilcox strata are faulted down against these fossiliferous Wills Point beds.

From an outcrop of strata lying near the top of the Kincaid formation on the right bank of Colorado River just below the Bastrop-Travis county line in Bastrop County *Epistominoides midwayensis* n. sp. is here described and compared with the genotype.

The specimens figured in this paper have been deposited in the author's private collection. Extra material has been distributed to the U. S. National Museum, the Cushman Laboratory, the British Museum (Nat. Hist.), and the Melbourne National Museum.

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* Plummer, Helen Jeanne, Foraminifera of the Midway formation in Texas: Univ. Texas Bull. 2644, 1927.

** Plummer, F. B., Cenozoic systems in Texas: Univ. Texas Bull. 3232, p. 530 et seq., 1932. The divisions of the Midway group now in use are here described. Kincaid formation is equivalent to the "basal Midway," and Wills Point formation to the "upper Midway" of H. J. Plummer, 1927.

Genus **Epistominoides** gen. nov.

The finely perforate, hyaline, involute, trihedral, and trochoid test is bilaterally unsymmetrical with chambers very little better exposed on the dorsal side. The aperture is a short elongate slit located on the periphery at the end of the septal face and bounded by ventral and dorsal projecting lips that merge posteriorly into the peripheral carina and anteriorly into the dorso-anterior angle of the trihedral test. As a new chamber is added, the aperture is covered by overlap and sealed, and a foramen is formed about midway in the septal face as it becomes a septum. Connected with the dorsal lip of the aperture is a thin and perforate wall that extends down into the final chamber across its ventro-anterior angle to the septum on the ventral side of the foramen (Pl. 24, fig. 3). This inner partition joins the ventral wall along a curved line that forms a supplementary suture from the posterior end of the apertural slit across the posterior angle of the ventral outline of the chamber (Pl. 24, 1a). It is connected to the septal face along a line that extends from the anterior end of the apertural slit in a direction about parallel to the ventral edge of that face to some point within the area of the face (Pl. 24, fig. 1b, and 3). This delicate inner wall is supported and reinforced along its free edge by a fold of the wall that extends from the ventral side of the foramen in the septum across the chamber to the septal face (Pl. 24, fig. 3). The inner partition thus forms a small vestibule through which the protoplasm must pass to gain exit from the shell.

Genotype, *Saracenaria wilcoxensis* Cushman and Ponton.

A comparison of the internal structures of *Epistomina* and *Epistominoides*, as exemplified by the genotypes, shows the two generic groups to be very closely related. More than a hundred large and perfect specimens of *Epistomina elegans* (d'Orbigny) from a dredging taken in the North Atlantic have offered exceptionally fine opportunity to view the position of the inner wall or partition of the final chamber through the glassy shell material without resorting to operations on the tests. In both *Epistomina* and *Epistominoides* the characteristic chamber partition is joined to the dorsal lip of the apertural slit (epistomine aperture), as shown by broken specimens (fig. 1, a and b). In *Epistomina elegans* the union of the partition with the dorsal lip was further proved by inserting into the final apertures of a large number of transparent specimens a fine wet brush, the hairs of which lay within the final chamber of each test between the ventral wall and the partition. In both genera the slit-like aperture on or near the periphery of the final chamber becomes obsolete as an aperture, either by sealing or by overlap, when a new chamber is added, and during this process of expansion a foramen forms in the septal face on the dorsal side of the partition as the septal face becomes the final septum. In both generic structures the anterior or free edge of the partition is characterized by a fold that swings around toward the ventral wall of the chamber (Pl. 24, fig. 2, 3; text fig. 1b and 1c). The essential difference in the internal characteristics of the tests of the two genera is in the position of the chamber partition; in *Epistomina* it falls as a slightly undulating curtain across the chamber in a direction parallel to the plane of coiling, whereas in

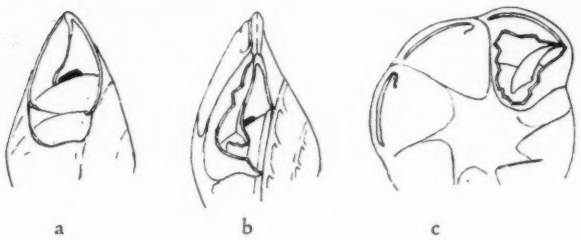


Fig. 1.—*Epistomina elegans* (d'Orbigny) from the North Atlantic, 51° 23′ 30″ N., 11° 47′ W., 620-695 fms. *a*, Peripheral view of a specimen broken across the penultimate chamber and showing the line of junction of the chamber partition with the septum, its union with the dorsal lip of the aperture, and its relationship to the foramen; the inner wall or partition itself has been resorbed and the aperture sealed; x25. *b*, Peripheral view of a specimen broken across the anterior portion of the final chamber and of the upper part of the partition; this shows the union of the partition with the dorsal lip of the aperture, the junction of this inner wall with the septum and with the previous whorl, and the position of the foramen; x50. *c*, Ventral view of a specimen showing the fold at the anterior and free edge of the partition; x50. This view was obtained through the transparent test, but for purposes of illustration the ventral wall is shown as broken away.

Epistominoides it lies diagonally across the ventro-anterior angle of the chamber. In *Epistomina* the inner wall is connected with the septum and with the previous whorl and therefore gives rise to no supplementary suture, whereas in *Epistominoides* its union with the ventral wall makes a very distinct supplementary suture across the posterior angle of the triangular chamber outline on the ventral side of the test, and its union with the septal face makes a distinct line part way across the outside of that area. Very close examination of large tests of *Epistomina elegans* reveal a very short union of the partition with the ventral wall of the chamber from the anterior end of the apertural slit, and this junction makes a small curved line on the ventral wall of each chamber (fig. 1c), a feature that corresponds to the longer and more conspicuous junction of the partition of *Epistominoides* with its septal face. The large glassy specimens of *Epistomina elegans* from the North Atlantic show that the partition exists fully intact only in the final chamber and is resorbed wholly or partially as new chambers are successively added. The specimens of *Epistominoides wilcoxensis* are not wholly convincing in this feature of development, but evidence is fairly clear that similar resorption probably takes place.

Many tests of the *Epistomina* characteristic of the Midway fauna were also studied, and these have been found to carry the same characteristics as those of *E. elegans* from the North Atlantic.

It is likely that the inner wall or chamber partition of *Epistomina* and *Epistominoides* is a protective device to prevent too ready exit of the protoplasm through a rather large and exposed aperture. The protoplasm passes readily from chamber to chamber through large foramina into the larger com-

partment of the final chamber, but to gain exit from the shell it must pass around the fold of the anterior edge of the partition and out through a comparatively narrow passageway or vestibule between the partition and the ventral wall to the aperture.

Epistominoides wilcoxensis (Cushman and Ponton)

Plate 24, figs. 1-3

Saracenaria wilcoxensis Cushman and Ponton, 1932, Contrib. Cushman Lab. Foram. Res., vol. 8, p. 54, pl. 7, fig. 9.

Test elongate, sharply trihedral, with septal face nearly as broad as ventral and dorsal faces, very nearly bilaterally symmetrical, involute but showing very slightly more of the coil on the dorsal side of the consistently left-handed spire; chambers 6 or 7 to the whorl, increasing successively in length at the rate of about 1.4, each one subdivided very unequally by a thin inner wall or partition that extends from the dorsal lip of the aperture obliquely across the ventro-anterior angle of the chamber and is attached to the septal face, to the ventral wall, and to the septum on the ventral side of the foramen; sutures flush to elevated, radiating from a boss on each side of the test, almost straight across both ventral and dorsal faces but curved sharply backward near the periphery; umbilical area filled with shell matter; aperture a narrow and elongate slit located in the peripheral angle of the final chamber at the end of the septal face and bounded by protruding ventral and dorsal lips.

Average length of Wills Point tests 0.5 mm.; average breadth 0.3 mm.; average thickness 0.25 mm. This size corresponds almost exactly to that of the typical Wilcox test.

A suite of about sixty Wills Point specimens shows considerable variation in the sharpness of the carination of the three lateral angles, in relative breadth of the septal face, and in the amount of departure from bilateral symmetry. The average size of the Wills Point specimens, their proportions, and the numbers of chambers per whorl fit closely the description and illustrations of the species named from Wilcox strata near Ozark, Alabama. Topotypes exhibit all the details of structure essential to the new genus *Epistominoides*, and they prove specific identity with the Wills Point form. Considerable variation in the development of the peripheral flange is apparent in a large suite of tests. In the Texas material the flange is well developed, though some few specimens are merely sharply carinate without any appreciable extension of the keel into a thin, transparent flange. The Wilcox test of this species at its type locality carries no flange or one that is weakly developed. This is a variation due to environmental conditions and is of no specific value.

E. wilcoxensis (Cushman and Ponton) has been observed in several outcrops of Wills Point strata from the rich clays of the Mexia clay member upward to a stratigraphic elevation almost 400 feet above the base of the formation. In Texas the species is probably diagnostic of the Midway group of strata, and so far it has been observed only in the Wills Point formation.

Epistominoides midwayensis sp. nov.

Plate 24, fig. 4

Test elongate, somewhat more than half as broad as long, strongly bilaterally unsymmetrical, umbilicate; periphery sharply carinate but not distinctly flanged; dorsal face gently convex, ventral face somewhat more convex; chambers 7-8 in the mature whorl, increasing successively at the rate of about 1.2, subdivided internally by a thin partition that extends from the short, slit-like aperture into each chamber across its ventro-anterior angle making by its junction with the ventral wall a supplementary ventral suture so close to the anterior edge of the chamber and no nearly parallel to it as to be somewhat obscure; septal face triangular, width about three-quarters the height and marked externally by the junction of the inner partition from the anterior end of the apertural slit part way across the septal face and parallel to its ventral edge; ventral sutures nearly straight and marked by a slight thickening of the ventral wall between each true suture and the paralled supplementary suture to form blunt ridges that radiate from a small umbilical depression; dorsal sutures narrowly elevated, radiating from a broad central boss, and sharply curved backward near the periphery; aperture a short elongate slit located on the peripheral angle at the end of the septal face and bounded by protruding ventral and dorsal lips.

Length of holotype 0.55 mm.; breadth 0.32 mm.; thickness 0.27 mm.

Epistominoides midwayensis sp. nov. is distinctly different from *E. wilcoxensis* (Cushman and Ponton) in having somewhat broader chambers and in being unbilicate, strongly bilaterally unsymmetrical, somewhat more compressed, and divided internally by chamber partitions that are so narrow and lie so close to the ventro-anterior angles of the chambers as to be almost imperceptible, especially since the wall is somewhat stouter and thicker than that of the genotype. Dampening the specimens brings out the salient features and even renders them sufficiently translucent to show the position of the fold of the partition in the final chamber.

This species has been observed at only one locality, which lies close to the top of the Kincaid formation of the Midway group. This outcrop* of glauconitic clay is in the right bank of Colorado River between the Travis-Bastrop county line and the mouth of Dry Creek in Bastrop County, Texas. About one-eighth of a mile downstream the *Venericardia bulla* bed, which marks the base of the Wills formation, outcrops for several hundred feet in the right bank.

Genus **Coleites** gen. nov.

Test elongate, trochoid, calcareous, hyaline, coarsely perforate; early chambers tightly coiled, mature chambers becoming uncoiled; aperture in early chambers an irregularly elliptical opening above the base of the septal face and

* Plummer, Helen Jeanne, Midway foraminifera in Texas: Univ. Texas Bull. 2644, p. 59, Station 67, 1927.

close to the periphery on the ventral side, gradually becoming terminal as chambers become more nearly rectilinear and developing a faint tooth on the ventral side of the elongate and narrow orifice; foramina connected by a tube which extends to the aperture of the final chamber.

Genotype, *Pulvinulina reticulosa* Plummer.

This genus has been named for W. Storrs Cole, who has contributed much to our knowledge of Tertiary formaninifera of Mexico and Florida.

Coleites reticulosus (Plummer)

Plate 24, figs. 5-9

Pulvinulina recticulosa Plummer, 1927, Univ. Texas Bull. 2644, p. 152, pl. 12, fig. 5.

Test broadly elongate, strongly compressed, flat or gently convex on the dorsal side, more convex on the ventral side, coarsely and irregularly reticulate on both sides except over the septal face; periphery very sharp and bounded by a ragged flange; early chambers tightly coiled through two or more convolutions, very narrow, curved, gradually lengthening, 7 in the final whorl; fully mature chambers short, broad, and rapidly becoming almost rectilinear; foramina connected by a stout tube, which in the final chamber extends to the aperture; early sutures completely obscured by the coarse reticulation of the test but clearly visible when test is mounted in liquid, strongly curved dorsally but somewhat less curved ventrally, later sutures very slightly constricted and not quite parallel; aperture of very young tests an elliptical opening on the ventral side of the peripheral angle above the base of the septal face, but with growth of the test the opening becomes more narrow and longer and develops a faint blunt tooth on its ventral edge.

Length of most mature test observed 0.85 mm. (Pl. 24, fig. 5), breadth 0.52 mm.; thickness 0.21 mm.

The length of the slit-like aperture varies somewhat in proportion to the test, and one specimen shows it to be slightly protruding from the peripheral outline. The flange is also variable in degree of development, as are most flanges. The blunt tooth that characterizes the aperture in this genus is clearly seen on well-preserved and opaque specimens of this species, but it is so delicate a feature, that it is almost impossible to observe in very translucent tests and is easily destroyed in preparation of samples. The degrees of lateral compression of the test in some places is greater than that indicated in the peripheral view here figured (Pl. 24, fig. 6).

Coleites reticulosa (Plummer) has been observed in several outcrops and well samples in the Wills Point formation of the Midway group, and in Texas it is probably restricted to strata of this age.

PLATE XXIV

FIGURES

1–3. *Epistominoides wilcoxensis* (Cushman and Ponton), x65, from Wills Point formation 2 miles north of Mexia, Texas.

1. Perfect specimen showing: *a*, ventral view; *b*, peripheral view; *c*, dorsal view.

2. Peripheral view of a specimen from which the final chamber has been broken away. The attachment of the base of the partition to the septum shows the position of the wall and its fold relative to the foramen.

3. View into the final chamber of a specimen that was broken along its dorso-anterior angle. This shows the attachment of the partition to the dorsal lip of the aperture and the relation of the partition to the septum, to the foramen, and to the outer walls of the final chamber.

4. *Epistominoides midwayensis* n. sp., x65, from uppermost part of Kincaid formation on right bank of Colorado River, just below the Travis-Bastrop county line in Bastrop County, Texas. *a*, Dorsal view of holotype; *b*, peripheral view; *c*, ventral view, showing supplementary suture on ventral face of final chamber very close to the ventro-anterior angle. On the ventral wall of the previous chambers this suture follows the posterior side of the thickened shell matter between the chambers, and the true suture follows the anterior side.

5–9. *Coleites reticulosus* (Plummer), x55, from Wills Point formation, 2 miles north of Mexia, Texas.

5. Ventral view of well-developed specimen with 4 chambers beyond the early trochoid coil. This shows the position of the mature aperture with its blunt tooth, the smooth septal face, and the typical reticulate ornamentation of the species.

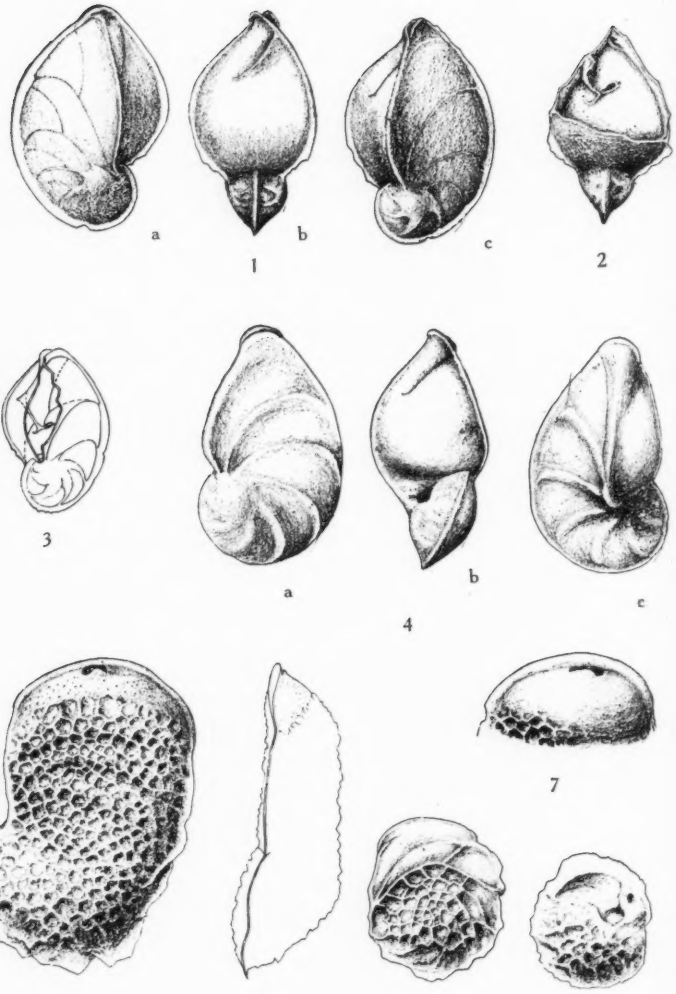
6. Peripheral view of the same specimen showing the relative biconvexity of the average test.

7. View of the second chamber beyond the early coil, showing an aperture somewhat more elongate than average.

8. Dorsal view of a young specimen still in the coiled stage. The somewhat weaker development of the reticulate ornamentation reveals the curvature of the chambers.

9. Ventral view of a youthful specimen from which the wall of the final chamber has been broken away to show the internal tube between the foramen and the elliptical aperture above the base of the septal face.

PLATE XXIV



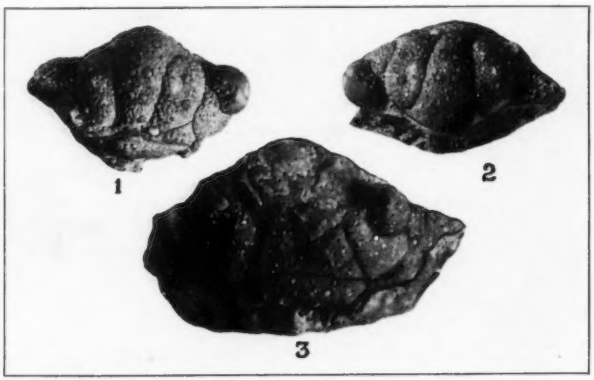
A NEW SPECIES OF DICRANOPELTIS

CAROL Y. MASON

I. Introduction

The Thomas A. Greene Collection of Silurian fossils of the Milwaukee and Chicago regions contains many trilobites, of which some have not hitherto been described. One of these, of the genus *Dicranopeltis*, we have named *greenii* in honor of the collector. The Greene Memorial Museum contains seventeen specimens of the species, showing slight variations but maintaining certain specific characters which show them to be a new species.

The species is placed in the genus *Dicranopeltis* because of the lobation of the glabella. The general appearance suggests that of *Dicranopeltis decipiens*, W. & M., as figured by Weller[1] but in nearly all specimens the third lateral glabellar lobe has united with the occipital lobe to form one nearly triangular lobe at the posterior end of the glabella. In the paratype a cast from Hawthorne, Illinois (Fig. 3) there is a quite definite though faint furrow on one of these lobes, dividing it into a third lateral and an occipital lobe. This feature is more pronounced on one of the impressions from Racine. Whether the presence or absence of this division between the lobes is the result of variation in preservation or in the animals themselves is



Figs. 1-2. Dorsal and anterior views of the holotype, cast of cephalon from Wauwatosa, Wisconsin, x 1.5 (156, Greene Memorial Museum.)

Fig. 3. Posterior-dorsal view of the paratype, cast of cephalon from Hawthorne, Illinois. x 1.5 (481, Greene Memorial Museum.)

1 WELLER, STUART: The Paleontology of the Niagaran Limestone in the Chicago Area, Part 2, The Trilobites, Chicago Academy of Sciences, Bulletin 4, p. 237, pl. 22, figs. 10-11, 1907.

uncertain, though the latter is more probable, since the holotype (Fig. 1), an exceptionally fine specimen, does not show the dividing furrows. That it is not a variation with age and size of the animal is shown by the fact that both divided and undivided lobes occur in large and small specimens. Since the lobes are divided in some cases, however, and the general arrangement of glabellar lobes is appropriate, the species is placed in the genus *Dicranopeltis*.

II. Description

Dicranopeltis greenii, sp. nov.

Description. — Cephalon sub-pentagonal, very convex, finely tuberculate. Glabella strongly defined. Median lobe widest in front, extending farther forward than lateral lobes and terminated by very narrow, well defined lip-like formation which scarcely projects but is continuous with ridge bounding anterior edge of free check. At junction of first and third lateral furrow, median lobe of glabella approximately one third its width at anterior end. This proportion varies somewhat with the individual, as does the degree of spread of the anterior end.

Dorsal furrows well defined, stronger in front, continuous in front of median lobe of glabella, extending straight back from anterior end of palpebral lobe about half way to occipital furrow, from which point they curve diagonally backward and outward, meeting occiptal furrow at points approximately one half the distance from median line to genal angles.

First lateral furrows defining median lobe of glabella from anterior margin four fifths of distance to occipital furrow, spreading anteriorly to form acute angles with dorsal furrows at anterior margin. Second lateral furrows obsolete or indicated by slight indentations approximately at center of the first. Third lateral furrows extending from posterior ends of first, diagonally forward to meet dorsal furrows at point where the latter turn diagonally backward and outward.

First two lateral glabellar lobes united to form sub-ovoid, convex single lobes, narrower at posterior extremities. Third lateral lobes and occipital lobes combined to form single sub-triangular nearly equilateral lobes, with apices at junction of third lateral and dorsal furrow, outer angles formed by meeting of dorsal and occipital furrows, inner angles undefined, the two lobes being continuous with posterior end of median lobe except for very slight grooves which continue posteriorly from first lateral furrows and disappear before reaching occipital furrow. On some specimens, including the paratype, a slight furrow separates a small triangular occipital lobe at the outer edge of one or both of these compound lobes, but in most specimens, including the holotype, this furrow is entirely absent.

Occipital furrow well defined, concave posteriorly to junction with dorsal furrows, thence curving forward. Length of occipital furrow from dorsal furrow to facial suture about three-fourths that from median line to dorsal furrow. Occipital segment convex, widest in center, tapering to axial furrow, about one-third as wide on pleural lobes as at center of axial lobe. Facial suture visible on these specimens only from eye posteriorly to occipital furrow,

which it meets about halfway between dorsal furrow and outer margin of free cheek.

Free cheek convex, sub-rectangular, extending outward and only slightly backward in genal or lateral spine, of which only a part is preserved. Eyes very prominent, opposite anterior ends of first lateral glabellar lobes and approximately one-third their size, nearly spherical but somewhat elongate diagonally backward toward genal angle. Lateral edges facing posterior part of median line of glabella, in a vertical palpebral lobe covered with tubercles. Visual surface smooth.

Four pairs of large tubercles occur on median lobe of glabella. Anterior pair equidistant from each other and from first lateral furrows. Distance from anterior to second pair greater than that from second to third pair. Distance between tubercles of second, third and fourth (posterior) pairs approximately the same. Two large tubercles on first lateral lobes opposite second and third pairs on median lobe, and three large tubercles on palpebral lobe. Others irregularly scattered.

Thorax and pygidium unknown.

Comparisons. — This species differs from *Dicranopeltis decipiens*, W. & M., a specimen of which was seen by the author at the Walker Museum, University of Chicago. The outstanding difference is in the union of third lateral with occipital lobes, to form one large triangular lobe which is more acute than the corresponding lobes of *D. decipiens*, the furrow bounding the anterior edge of the large lobe of the new species being more diagonal while the corresponding furrow of *D. decipiens* is nearly parallel with the general trend of the posterior edge of the cephalic shield. Where a distinct occipital lobe is present, in the new species, it is longer than that of *D. decipiens*, being a nearly equilateral triangle while that of *D. decipiens* is nearly three times as wide as long. Even where the occipital lobe is present in the new species, in no instance does the occipital furrow definitely divide to form it.

The large conspicuous eye is another distinction, although the eye of *D. decipiens* is not preserved. The united first and second lateral lobes are narrower than in *D. decipiens*, and the palpebral lobe meets the anterior portion of the dorsal furrow. The genal spine projects more laterally and less posteriorly than that of *D. decipiens*. The regular placement of large tubercles is a further difference.

The species differs from *Dicranopeltis arkansana* Van Ing., in position of eye, shape of free cheek, and position of tubercles on the glabella. The glabella of *D. greenii* is also shorter, with combined first and second lateral lobes less pear-shaped, and third lateral lobes where present much more rectangular than those of *D. arkansana*.

Occurrence. — Racine Dolomite (Niagaran: Guelph) at Racine, Milwaukee and Wauwatosa, Wisconsin; and at Hawthorne, Ill.

Holotype. — 156; Paratype. — 481, Greene Memorial Museum, Milwaukee-Downer College.

GREENE MEMORIAL MUSEUM,
MILWAUKEE-DOWNER COLLEGE.

SOME ATLANTIC COAST TERTIARY PECTINIDAE

H. I. TUCKER

Acknowledgements

The writer is indebted to Dr. Paul Bartsch, of the United States National Museum, for the privilege of studying type specimens deposited in the Museum collections. Dr. W. C. Mansfield, of the United States Geological Survey, kindly permitted the writer to study material in his collections and offered many helpful suggestions.

Description of Species

Genus PECTEN Müller, 1776

Type, by subsequent designation, Schmidt 1818, *Pecten maximus* Linné.

Pecten (Pecten) wendelli sp. nov.

Pl. 25, fig. 1.

Description: Shell very thin, equilateral, suborbicular. A single strong radial cord extends nearly to the beak anteriorly and another posteriorly; three weaker, equally spaced cords lie between the secondary cords and become obsolete 2 mm. from the margin of the disk. Fine, concentric lines extend straight across the radials. Submargins plain, narrow, steep. Auricles large, probably subequal, with about 7 fine, scabrous radial threads. Internal margin of the shell grooved for about 2 mm. Provinculum; auricular crura. *Dimensions:* height 14, width 13 mm. This species is named in honor of Dr. W. C. Mansfield of the United States Geological Survey.

Remarks: This species differs from *P. leonensis* Mansfield very markedly in sculpture. The greater portion of the disk of *wendelli* has only concentric sculpture of fine lines while the whole disk of *leonensis* has strong radial sculpture. The concentric lamellae are reflected away from the beak on the summits of the ribs of *leonensis*, while on *wendelli* the lines pass directly across the radials. The concentric sculpture of *wendelli* is much weaker and the shell is more nearly orbicular.

Occurrence: Caloosahatchie Pliocene. Ft. Denaud, Fla.

Holotype: A left valve. Collection H. I. Tucker.

Pecten (Pecten) brouweri sp. nov.

Pl. 25, figs. 4, 5.

Description: Shell equilateral, very inequivalved, the right valve strongly convex, well developed radial sculpture. On the right valve 14 broad, flat-topped primary and two secondary ribs at each submargin. Each primary rib has a cord on the summit, extending from the umbonal region to the margin of the disk. Fine, concentric, crowded imbrications on disk tend to become coarser and more conspicuous in the umbonal region. Interspaces flat, about half as wide as the primary ribs. Margins scalloped. Submargins narrow, steep, without ornamentation. Auricles nearly equal; 5 to 6 radials, which become obsolete near the beak. Left valve very slightly concave; 13 high, rounded ribs which develop a median sulcus about 14 mm. from the

ventral margin of the disk. A single intercostal between two of the ribs on the anterior portion of the disk. Near the beak the ribs tend to become nearly obsolete. Fine, closely spaced, concentric sculpture over the disk and auricles. No radials on the submargins. Ribs about half as wide as the flat interspaces. One radial on each of the subequal auricles. *Dimensions.* — right valve, height 43, width 46 mm.; left valve, height 41.5, width 45 mm.; diameter 21 mm. This species is named in honor of Professor H. A. Brouwer, of Der Universiteit van Amsterdam.

Remarks. — *P. brouweri* differs from *P. raveneli* Dall in width of interspaces, convexity, and number of ribs. The interspaces of *raveneli* are scarcely more than sulci; commonly has 22 ribs; much stronger, uniform, and coarser concentric sculpture than *brouweri;* the left valve of *raveneli* is more concave than that of this species.

Occurrence. — Waccamaw Pliocene. Walkers Bluff, N. C. (type); Nixon's Landing, N. C., Dr. Burnett Smith.

Cotypes. — Right and left valves of the same individual. Collection H. I. Tucker.

Paratypes. — Deposited in the collection of the Paleontological Research Institution, Ithaca, New York, by Dr. Burnett Smith.

Genus CHLAMYS Bolten, 1798.

Type, by subsequent designation, Herrmannsen 1846, *Pecten islandicus* Linné.

Chlamys (Chlamys) dehayesi dennisoni subsp. nov.
Pl. 26, fig. 1.

Pecten dehayesii Lea, var., Harris, Bull. Am. Pal., vol. 6, pl. 13, fig. 1, 1919.

Description. — Shell large, heavy, orbicular, convex, slightly inequilateral; beak pointed, shell expands rapidly in width. Sixteen strong, simple, rounded ribs which are wider than the flattened interspaces. Single thread on the summit of each primary rib extends about 20 mm. from the margin of the disk toward the beak. One strong radial thread in center of each interspace with a secondary on either side near the base of the adjoining rib. Concentric sculpture of overlapping lamellae which are elevated on the intercostals and on the summits of the ribs. Submargins wide, sculptured with fine, closely spaced, scabrous radial threads. Subequal auricles have the same type of sculpture. Interior ribbed to correspond to the external interspaces. *Dimensions:* height 42, width 41, hinge 22 mm. This subspecies is named in honor of Professor G. D. Harris, of Cornell University.

Remarks. — This subspecies is much larger than *C. dehayesii* Lea, more circular in outline, simpler sculpture, and is less convex in the umbonal region. It is conspicuous because of its unusual size as compared with other Eocene species.

Occurrence. — Claiborne Eocene. Claiborne, Ala.

Holotype. — A left valve. Collection Paleontological Research Institution, Ithaca, New York.

Chlamys (Chlamys) sheldonae sp. nov.
Pl. 27, fig. 2.

Description. — Shell thin, subovate, very inequilateral, convex, strongly sculptured, auricles unequal. Sixteen primary ribs, which in the umbonal region are simple, rounded, narrower than the interspaces. About 8 or 10 mm. from the ventral margin the ribs tend to develop a marked sulcus on their summits, and frequently become dichotomous. At about the same point there appear from 1 to 3 scabrous intercostals. Usually the primary ribs develop a single row of conspicuous, fluctuated scales on their summits before they become sulcate. On the anterior and posterior portions of the disk the scaly threads alternate in strength, becoming finer toward the submargins, the auricles, and in the interspaces. Six to seven radiating, scaly threads on the auricles. Fine provinculum. Margin of disk crenulated, obsolete grooves extend nearly to the beak. *Dimensions:* height 22, width 18, convexity 6 mm. This species is named in honor of Dr. P. G. Sheldon, of Ithaca, N. Y.

Remarks. — This species has fewer ribs and stronger camptonectes marking then *C. choctavensis* Aldrich. That species lacks the strong scabrous sculpture so well developed in *sheldonae*. *C. choctavensis* is equilateral, *sheldonae* quite inequilateral.

Occurrence. — Aquia Eocene, Ft. Washington, Md.

Holotype. — A left valve. Collection Paleontological Research Institution, Ithaca, New York.

Chlamys (Chlamys) beverlyi new name.

Pecten (Chlamys) gilbertharrisi Tucker, Ind. Acad. Sci., Proc., vol. 40, p. 243, pl. 1, fig. 1, 1931.

Discussion. — This name is preoccupied by *gilbertharrisi* F. and H. Hodson. I therefore propose the name *C. beverlyi* Tucker for this species.

Occurrence. — Jackson Eocene. Lisbon, Ala. (type); Sabine River, below Robinson's Ferry, La.

Chlamys (Chlamys) crocus Cooke.
Pl. 25, fig. 3.

Pecten crocus Cooke, Carnegie Inst. Wash., Publ. No. 291, pt. 4, p. 135, pl. 9, figs. 2a, b; pl. 11, fig. 9.

Description. — The Florida shells are not so high in proportion to their width as the Anguilla specimens. The intercostal is nearly as wide as the interspaces. Spiny sculpture well developed on the central part of the disk near the ventral margin and on the anterior and posterior portions of the valves. Auricles somewhat larger than those of the holotype, unequal; scabrous, fine radial sculpture. Distinct fasciole; shallow byssal notch. Ctenolium of about three denticles. Internal margin of shell grooved. It is probable that these differences are within the normal range of variation for this species. *Dimensions* of figured shell: Height 40, width 28 mm.

Occurrence. — Tampa Miocene. Crocus Bay, Anguilla, Cooke (type); Six Mile Creek, Fla.

Holotype. — Collection United States National Museum, Cat. No. 167079.

Plesiotypes. — Collection H. I. Tucker.

Subgenus LYROPECTEN Conrad, 1862.

Type, by subsequent designation, Dall 1898, *Pallium estrellanum* Conrad.

Chlamys (Lyropecten) santamaria sp. nov.

Pl. 26, fig. 2.

Description. — Shell equilateral, suborbicular, inequivalved. Radial sculpture of 12 to 16, most commonly 12 to 14, broad, well elevated ribs which are approximately 4 mm. narrower, at the ventral margin, than the interspaces. Right valves commonly have about 12 ribs which are about 2 mm. narrower than the interspaces. The right valves are flat, or nearly so, and resemble *C. madisonius*. Say very closely in outline; left valve convex in the umbonal region; auricles subequal, radial sculpture of fine, scaly threads, the anterior the more coarsely threaded; fasciole broad. Auricles of the left valve subequal, uniformly sculptured with fine scaly threads. Summits and sides of the ribs threaded with numerous fine, scaly threads. Interspaces similarly ornamented; one or two of the threads are usually more strongly developed, especially on the right valve. Submargins have a fine uniform sculpture of closely spaced, scaly threads. Interior ribbed to the umbones. Provinculum presen. Ctenolium retained throughout the life of the individual. *Dimensions:* right valve, height, 130, width 126 mm. (figured shell); left, height 120, width 115 mm.; convexity 33.5.mm.

Remarks. — This species has the characteristic sculpture of *C. jeffersonius* Say and in outline closely resembles *C. madisonius* Say. It is separated from *jeffersonius* by the deep byssal notch, longer right anterior auricle, retention of the ctenolium in adult valves. It differs from *madisonius* in its finer, more uniform, scabrous sculpture; broader, flatter ribs, shorter byssal auricle.

It is possible that this species may be related to both *madisonius* and *jeffersonius*. *C. madisonius* occurs first in the Chipola Miocene, while *C. jeffersonius*, s.s., appears in the lower Yorktown. The stronger development of some of the intercostals and the shortening of the byssal auricle suggest a possible relationship through *edgecombensis*.

Occurrence — St. Mary's Miocene. St. Marys River, Md. (type); Chancellor Pt. and Langleys Bluff, Md.; Snow Hill, Green County, N. C.

Cotypes. — Right valve, collection Paleontological Research Institution, Ithaca, New York. Left valve, United States National Museum, Cat. No. 2498. The valves are from the same locality.

Paratype. — A right valve, United States National Museum, Cat. No. 2498. *Dimensions:* Height 101, width 79 mm. An imperfect shell.

Chlamys (Lyropecten) pontoni Mansfield.

Pecten madisonius Say, Mansfield, U. S. Nat. Mus., Proc., vol. 51, p. 601, listed from Red Bay, Fla., 1916.

Chlamys (Lyropecten) pontoni Mansfield, Fla. Geol. Surv., Bull. No. 8, p. 59, pl. 10, figs. 1, 2, 1932.

Discussion. — If the Vaqueros formation of California is correctly assigned to the lower Miocene, it is possible that *C. magnolia* Conrad may be related to the east coast *C. jeffersonius* through *pontoni*. Comparison of Conrad's types of *magnolia* does not indicate any close relationship with

jeffersonius, s.s., such as Grant and Gale, Mem. San Diego Soc. Nat. Hist., vol. 1, p. 176, 1931, suggest. *C. jeffersonius* does not appear in the Atlantic Tertiary before the Choctawhatchee (lower Yorktown). These specimens have from 7 to 9 ribs and the characteristic sculpture of *jeffersonius*. Typical *jeffersonius* has from 9 to 10 ribs; *magnolia*, 11 ribs. *C. jeffersonius*, s.s., is more equilateral, equivalved, the ribs are more uniform in size over the disk and the shell does not slope so much anteriorly and posteriorly as does *magnolia*.

Comparison of *magnolia* and *jeffersonius* shows no valid reason for considering them to be the same species. It is unfortunate that the California shells assigned to the eastern species were not figured.

Occurrence. — Choctawhatchee Miocene. Red Bay, Walton County, Fla., Mansfield.

Holotype. — United States National Museum, Cat. No. 371613.

Subgenus AEQUIPECTEN Fischer, 1886.

Type, by monotypy, *Ostrea opercularis* Linné

Chlamys (Aequipecten) burnetti sp. nov.

Pl. 25, fig. 2.

Description. — Shell equilateral; radial sculpture well developed; the valves somewhat flat, the left the more convex. The right valve has sixteen rounded ribs; the left, fifteen somewhat sharper ribs. A sulcus appears on the summits of the ribs 10 to 15 mm. from the ventral margin. A single intercostal appears on the right valve 3 or 4 mm. before the groove on the primary ribs. On the left valve there is one, rarely two, smaller intercostals. Interspaces on the left valve much the wider. Concentric lamellae stronger on the left valve. Submargins plain. Auricles of left valve lamellated; 4 to 5 radial threads; right anterior auricle has 3 radial threads, posterior, 5. Very wide byssal fasciole. Ctenolium present. Interior ribbed. *Dimensions.* — height 33, width 27 mm. This species is named in honor of Dr. Burnett Smith.

Remarks. — This species differs from *C. perplanus* Morton in having fewer ribs, smaller auricles, less marked scaly sculpture, and in the absence of a provinculum. This species has 15 to 16 ribs while *perplanus* has 23 to 25.

Occurrence. — Tampa Miocene. Six Mile Creek (type) and Black Water Creek, Florida.

Holotype. — A right valve. Collection H. I. Tucker.

Section PLAGIOCTENIUM Dall, 1898.

Type, by original designation, *Pecten ventricosus* Sowerby—*P. gibbus* var. *circularis* Sowerby.

Chlamys eboreus walkerensis subsp. nov.

Pl. 27, fig. 3.

Description. — Shell thin; very inequilateral; larger than typical *eboreus;* auricles smaller, nearly equal. Usually 20 low, rounded,widely spaced ribs.

Some specimens have 24 ribs. Concentric sculpture of wavy, elevated lamellae which are much more closely spaced from the umbonal region to the ventral margin. The ribs on very large shells become nearly obsolete at the margins. Valves nearly equally convex; margins scalloped. Only concentric sculpture anteriorly and posteriorly. At the posterior margin the left valve is markedly depressed and produced. *Dimensions.* — height 88, width 113, hinge 41.5, convexity 23 mm.

Remarks. — *C. eboreus* Conrad, s.s., from the type locality is more equilateral and more strongly ribbed. However, valves vary widely and this subspecies represents the extreme of a line of development. This subspecies has fewer ribs, usually; is commonly more strongly lamellated and has the characteristic depression in the posterior portion of the left valve.

Occurrence. — Waccamaw Pliocene. Walkers, N. C. (type); Nixon's Landing on Waccamaw River, S. C., Dr. Burnett Smith.

Holotype. — A left valve. Collection Paleontological Research Institution, Ithaca, New York.

Paratypes. — From Nixon's Landing, S.C., Collection Dr. Burnett Smith, Skaneateles, New York.

Section PLACOPECTEN Verrill, 1899.

Type, by original designation, *Pecten clintonius* Say.

Chlamys (Placopecten) virginianum Conrad.

Pecten virginianum Conrad, Foss. Med. Tert., p. 46, pl. 21, fig. 10, 1840. Heilprin, Acad. Nat. Sci. Phila., Proc., vol. 33, p. 420, 1881.
Pecten tenuis Lea, Am. Phil. Soc., Trans., vol. 9, p. 426, pl. 35, fig. 33, 1845 Conrad, Acad. Nat. Sci. Phila., Proc., vol. 14, p. 581, 1862.
Pecten (Placopecten) virginianus Conrad, Dall, Wag. Free Inst. Sci., Trans., vol. 3, pt. 4, p. 728, *partim*, 1898.
Pecten (Placopecten) marylandicus Wagner, Dall, Wag. Free Inst. Sci., Trans., vol. 3, pt. 4, p. 728, *partim*, 1898.

Discussion. — The holotype of *C. tenuis* Lea, United States National Museum, Cat. No. 145131, from Shell Bank, plantation of E. Ruffin, near Petersburg, Va., is certainly a worn left valve of *virginianum*. The sculpture and outline are so typical that there is no reason for considering it even a subspecies.

Occurrence. — St. Marys and Yorktown Miocene. Evergreen, Bellefield, and Ruffins Creek, Va.; Murfreesboro Landing, Meherrin River, N. C.; City Point, Va., Ruffin.

Genus AMUSIUM Bolten, 1798.

Type, by subsequent designation, Schumacher, 1817, *Amusium japonicum* Linné.

Subgenus PSEUDAMUSSIUM (Klein) Mörch, 1853.

Type, by absolute tautonomy, *Pecten septemradiatum* Müller.

Amusium (Pseudamussium) hamiltonensis sp. nov.
Pl. 27, fig. 1.

Pecten (Chlamys) clarkeanus Aldrich, Dall, Wag. Free Inst. Sci., Trans., vol. 3, pt. 4, p. 739, *partim*, 1898.
Pecten clarkeanus Aldrich, Harris, Bull. Am. Pal., vol. 6, p. 25, *partim*, pl. 15, figs. 10, 11, 12, 1919.

Description. — Shell somewhat thin; valves nearly equally convex and discrepantly sculptured. Right valve resembles *scintillatus* Conrad in outline. Beak pointed, faint radial striations best developed over the central portion of the disk; concentrically sculptured. Auricles subequal, the right has 4 radials, the left is plain. The left valve slightly more convex than the right; having the quinque-costate structure noted by Harris. Sculpture perhaps slightly stronger on this valve. Extending back from the beak about 7 mm., the concentric and radial sculpture intersect, giving the shell a somewhat cancellate appearance. Disk obscurely striated radially. Concentric sculpture rather stronger than on the right valve. Auricles subequal, the posterior auricle has 4 radials, the anterior none. At the point where the auricles are attached to the disk there is a row of close set, elevated, rounded scale-like processes which are evidently formed by the continuation of the concentric sculpture of the disk. This character seems to be present in none of the related species. The holotype shows only traces of obscure camptonectes striation on the submargins. *Dimensions.* — height, 21, width 19 mm.

Two young valves from Talahatchee, Miss. may belong to this species. They show cancellate sculpture over the entire disk and strong camptonectes marking. The larger left valve, height 9 mm., has five strong radials on the posterior auricle, three feeble ones near the submargin on the anterior. The posterior one has the cancellate sculpture of the disk.

Remarks. — This species is separated from *scintillatus* by its sculpture. That species is never radially sculptured, has much more strongly developed camptonectes sculpture, and never has the row of scales at the base of the auricles of the left valve. It is separated from *clarkeanus* by its much less well developed radial sculpture. Some specimens of *clarkeanus* have the cancellate sculpture on the beaks of the left valves, but all such specimens examined show the fairly strong radial ribbing at the margin of the disk, sometimes also on the anterior and posterior slopes of the disk. Aldrich states in the description of *clarkeanus* that it combines the characters of two subgenera. Certainly the holotype of this species should be referred to *Pseudamussium*, while the strongly ribbed forms referred to *clarkeanus* are properly included under *Chlamys*.

Occurrence. — Claiborne Eocene. Hamilton Bluff, Ala. (type); Talahatchee, Miss.

Holotype. — A left valve. Collection Paleontological Research Institution, Ithaca, New York.

Paratype. — A right valve from the type locality.

Dimensions: Height 20, width 16 mm. Collection Paleontological Research Institution, Ithaca, New York.

LABORATORY OF PALEONTOLOGY,
CORNELL UNIVERSITY,
ITHACA, N. Y.

PLATE XXV

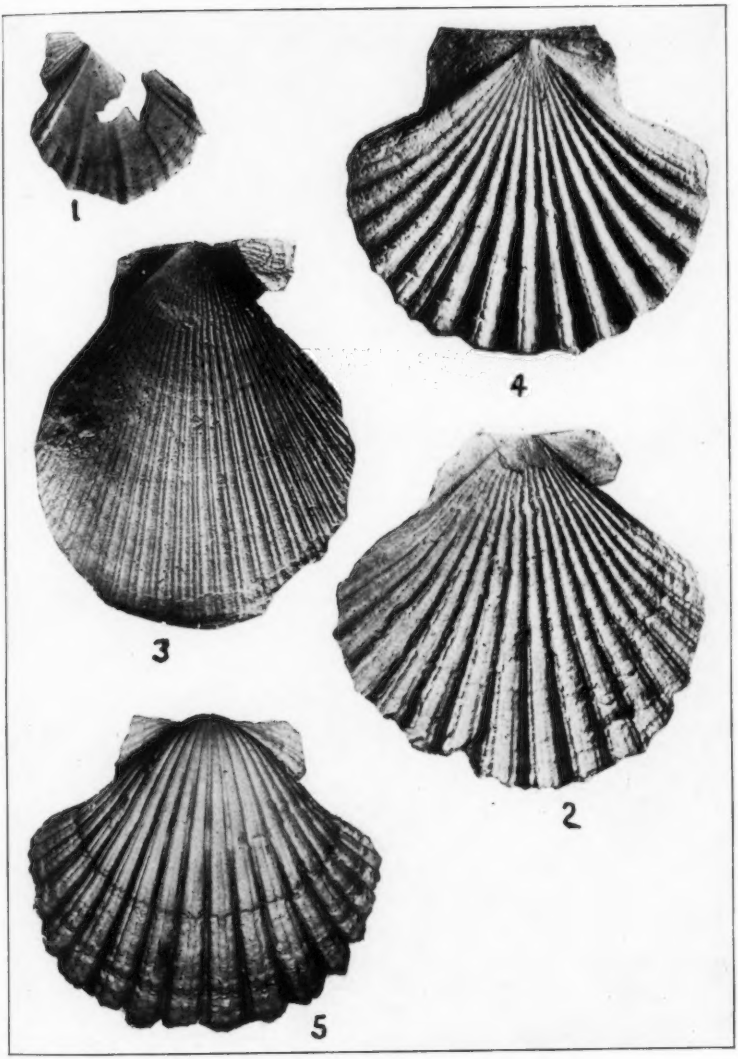


Fig. 1. *Pecten (Pecten) wendelli* Tucker, sp. nov. Holotype.
Fig. 2. *Chlamys (Aequipecten) burnetti* Tucker, sp. nov. Holotype.
Fig. 3. *Chlamys (Chlamys) crocus* Cooke. Plesiotype.
Figs. 4, 5. *Pecten (Pecten) brouweri* Tucker, sp. nov. Cotypes.

PLATE XXVI

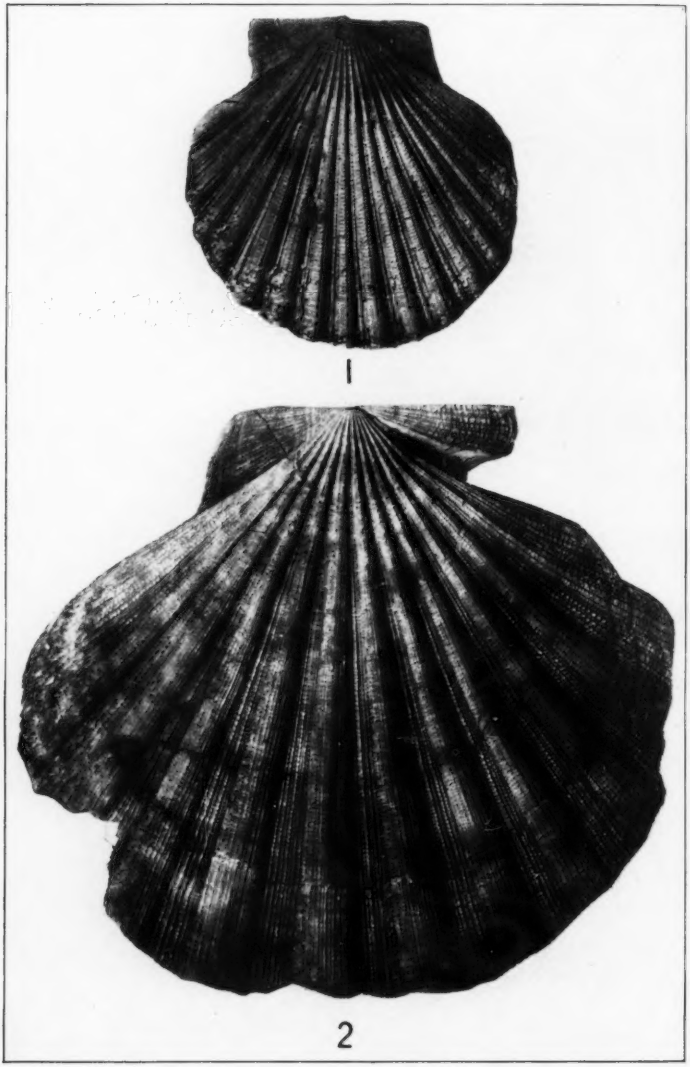


Fig. 1. *Chlamys (Chlamys) dehayesi dennisoni* Tucker, subsp. nov. Holotype.
Fig. 2. *Chlamys (Lyropecten) santamaria* Tucker, sp. nov. Cotype.

PLATE XXVII

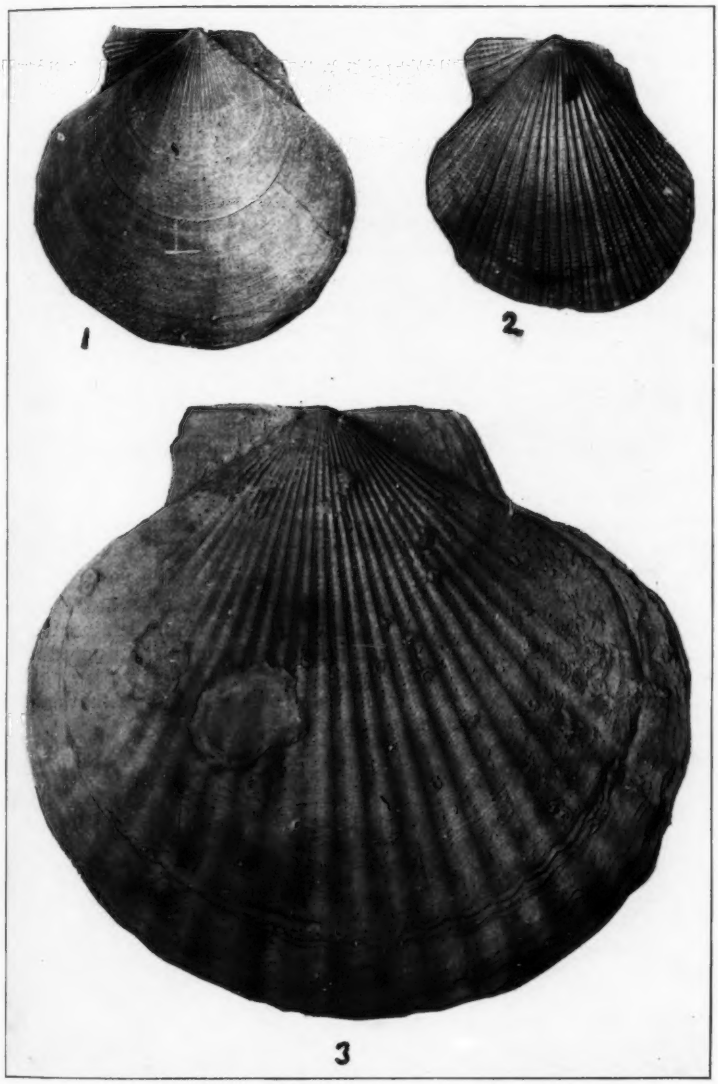


Fig. 1. *Amusium (Pseudamussium) hamiltonensis* Tucker, sp. nov. Holotype.
Fig. 2. *Chlamys (Chlamys) sheldonae* Tucker, sp. nov. Holotype.
Fig. 3. *Chlamys eboneus walkerensis* Tucker, subsp. nov. Holotype.

HYPERTROPHY IN THE JAW OF AN OKLAHOMA PROBOSCIDEAN

J. WILLIS STOVALL AND C. STUART JOHNSTON

The fossil to be discussed here is the left ramus of *Elephas imperator*, University of Oklahoma Museum No. 558. It was found in a Pleistocene gravel pit eight feet below the surface, at Lawton, Oklahoma.

Pathological conditions are frequently observed in fossils. In the University collection are ribs and other bones that show evidence of having been broken and healed. Bony growths are not infrequently seen, and also infections of the bone tissue, or of the periosteum may leave their fossil evidence. Young and Cooper* have described a number of cases in paleopathology, and pointed out the fact that certain diseases of early origin are continuing to exist, and may be recognized in animals now living. Romer**, in his discussion of exostosis in a fossil canid, calls attention to a condition, thought to be pathological, but which had been erroneously interpreted. In this case radial exostosis was reported in a number of individuals of the same species. The bony growth was similarly located in all cases, and in no instance was the remainder of the skeleton affected. Here the exostosis was not of pathological origin, but was a normal anatomical feature of this particular species.

In the fossil proboscidean with which this discussion is concerned, there are several features of more than usual significance. First, in the left ramus a great hypertrophy has taken place, which has given rise to a bulbous appearance to the lower side of the jaw (fig. 1). Second, part of the jaw and molar show unmistakable signs of having been badly abscessed. And third, the surface of the bone was infected over a wide area.

Fig. 1.—Anterior view of left ramus of *Elephas imperator* from Lawton, Oklahoma, showing hypertrophy on the ventral side.

* Young, Frank B., M. D., and Cooper, Albert L., M. D. A Study in Paleopathology, Radiology, March 1927.

** Romer, A. S., A Radial Exostosis in the Fossil Canid *Daphoenus*, Amer. Jour. Sci., vol. 8, September 1924, pp. 235-240.

The inferior dental foramen is 40 mm. in diameter, and appears normal. Coming to a point well within the foramen and below the level of the outer surface of the bone, is a cone-shaped growth of cancellous bone tissue of pathological origin.

A section of bone 220 x 122 mm. midway of the molar, on the inner side of the ramus, adjacent to the molar was cut away so as to expose the alveolar space. Immediately below the tooth there is a space of 144 mm., which is occupied by more or less dense cancellous bone tissue, the pores of which are about .5 mm. in diameter. It appears that there is an excess of this bone tissue below the tooth about 70 mm. in thickness.

The molar is complete, and in place. Its surface is evenly worn. Posterior to the worn grinding surface, the tooth is cracked through, and along this fracture plane there are signs of wear as though there had been considerable movement along the plane prior to the animal's death. On the inner posterior side of the tooth there is a large cavity, due to infection, the margin of which shows signs of having been partly healed. The healing here is indicated by what appears to be a secondary deposit of cement over a portion of the diseased tissues of the tooth. The vertical distance from the grinding surface of the molar to its base is 160 mm. At the base there are a number of root-like processes which are inclined in a backward direction from the tooth, and which seem to be normal. Figure 2 illustrates the ramus with the section of bone removed.

Fig. 2.—Inner view of the left ramus of *Elephas imperator* from Lawton, Oklahoma, showing: a, inferior dental foramen; b, opening in the jaw due to the abcess; c, fracture through the posterior part of the molar; d, interior of jaw with a portion of the bone removed. Length 628 mm., depth 274 mm.

On the inner side of the jaw, and at the angle of the ascending ramus is an opening cutting the inferior dental canal, and extending into the base of the molar. The dimensions of this opening are 110 x 85 mm. The texture of the bone in this region shows that it has not been broken away, and that it was the bony margin of the region occupied by a large abscess extending

from the surface to well within the interior of the tooth. This is also shown in figure 2.

Just posterior to the opening caused by the abscess, and at a point about 85 mm. below the inferior dental foramen there is a condition of existosis. This occupies an area of approximately 30 x 50 mm., and marks the point where the canal is cut through by the abscess. The bony growth rises to a height of 20 mm, above the canal.

A major portion of the ramus appears to have been affected with periostitis. The evidence for this lies in the fact that the surface of the bone over a wide area is abnormal, being very uneven, having numerous rugosities and depressions. Also it is of interest to note that many small foramina appear at the surface in this infected area, there being as many as three to the square centimeter in some places. Elsewhere they are not so numerous. These openings are all about 3 mm. in diameter.

It is, of course, impossible to know the cause of this pathological condition. It seems sufficient to remark that the results of the disease, as described, are in many ways similar to those found in animals now living.

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BOOK REVIEWS

A TEXTBOOK OF GEOLOGY. PART II—HISTORICAL GEOLOGY, by Charles Schuchert and Carl O. Dunbar. New York: John Wiley and Sons, 1933. vii + 551 pp, 332 figures. $4.00.

HISTORICAL GEOLOGY, by Raymond C. Moore. New York: McGraw-Hill Book Co., 1933. xii + 673 pp., 413 figures. $4.00.

THE PRINCIPLES OF HISTORICAL GEOLOGY FROM THE REGIONAL POINT OF VIEW, by Richard M. Field. Princeton: University Press, 1933. xii + 283 pp., 108 figures. $3.50.

These books have a common subject: the history of the planet earth. Yet they show surprising diversity in material, emphasis and objectives, as well as in mere style and form. So significant are these differences that they seem to demand discussion as well as review—discussion directed toward trends in the uses and teaching of geology in a period when geologists are superabundant, and when natural and physical sciences are yielding ground to the social.

One turns first to Schuchert and Dunbar, because of their work's established reputation. In title, at least, it is eighteen years old; during that period it has done much to disprove Salisbury's statement that "when knowledge dies, we bury it in textbooks." Have the contributions of a new author done as much in matters of viewpoint?

One first notices physical improvement: many new figures excellently printed, paleogeographic maps developed in relief, plates in halftone instead of coarse line. There are corresponding changes in substance, apparently directed toward the beginning student, for whom the volume avowedly is prepared. Facts are grouped about principles, and these (rather than data) are stressed. Without resort to dramatic language, there is a tone of action in which planets, rocks and organisms are interrelated factors. Continuity has been preserved by rearrangements of strictly biologic material into an appendix, and by more successful fusion of paleontology with geologic history. Despite emphasis on fossils, physical changes furnish the keynote to periods, and the number of maps illustrating these changes has been considerably increased. Granting the element of subjectivity in such maps, they still present justifiable generalizations, of importance to biogeography. Indeed, it would be hard to find a volume more suited to handy reference by biologists (especially zoologists) than this; and its use will prevent such glaring errors as are found in the work of Thomson and Hurst. Even extremists in land bridges will find it restraining, though Eria, Gondwanaland and Lemuria remain. Evidently there is need for extension of Matthew's work on terrestrial dispersal, and investigation of marine avenues and barriers, to determine whether these bridges may survive. The newly developed branch of paleoecology may be of value here.

The chapters themselves follow time-tried chronologic order. After preliminaries on fossilization and evolution, they progress to theories of earth origin, the geologic time table, and the length of geologic time table, and the length of geologic time. Here also is material of importance to biology, and to the general world-outlook that is supposed to result (but rarely does) from the study of historical geology. As an instance of the former: if the amount of salt in the sea is wholly out of keeping with the Planetesimal Hypothesis, does the retreat of primitive forms *(Plumatella, Spongilla* etc., studied by Pearse, Twitchell and others) to fresh waters find its background in an originally molten surface? Does the acknowledged variation in saltiness of blood have a similar background?

Pre-Cambrian eras are grouped into the Cryptozoic Eon, a division whose biologic basis may be sound, but whose physical unity seems questionable. The treatment of it is rather confusing, being partly regional and partly chronologic, with no clear division. Nor does the use of "system" on page 106 help matters; if a system is the rocks of a period, how can three systems be contemporaneous, as are Keweenawan, Grand Canyon and Belt in that table? Though it is possible that the Belt-Grand Canyon series extends below the Keweenawan, one hardly can grant that they also cover the period of Penokean orogeny to the beginning of the Cambrian, as this table implies. Should not the great pre-Cambrian unconformities of the Grand Canyon and Montana be assigned to the Penokean interval?

Treatment of Paleozoic and later periods is much more satisfactory, with a sense of proportion that has not always marked historical text books. Thus the Paleozoic receives 176 pages, the Mesozoic 87, and the Cenozoic 88. That man receives an additional 22 pages is in keeping with Professor Schuchert's Psychozoic era, retained in the general table of geologic chronology, but not popular with most glaciologists and mammalogists. The presence of this chapter is in keeping also, with the objective of teaching beginners—though even with reduced pages and improved organization, one wonders at the scope of beginning geology at Yale.

A corresponding chapter is less in place in Professor Moore's *Historical Geology*, apparently written for advanced students. At least, it makes no special concessions to the beginner, and avoids those devices by which his interest may be most readily aroused—albeit at some sacrifice of knowledge. Even paleogeographic maps are omitted on the ground of subjectivity. Since the limitations of such maps generally are considered by those who use them, this seems to be loss rather than gain. The text calls attention to just those physiographic features which appear on Schuchert's maps, but they do not appear on the outcrop and "inferred distribution" maps contributed by R. T. Chamberlin and others.

Earth origin and primitive development are treated rather fully, with emphasis on the work on T. C. Chamberlin. Wegener's hypothesis is briefly stated and rejected; there is adequate though brief treatment of Bailey Willis' hypothesis of asthenoliths. Both are of biologic importance, and should be considered by those who still think in terms of steady shrinkage of a cooling globe. The historical significance of rock characters is developed from the Grand Canyon region, one well suited to the purpose by its structure, sediments and availability.

There is no attempt to group Pre-Cambrian eras into a united time unit. A general chapter discusses the "oldest known rocks" and there is one each for Archeozoic and Proterozoic, the latter receiving 22 pages. Five Proterozoic periods are recognized (Temiskaming, three Huronian, and Keweenaw), with the implication that Belt and Grand Canyon "series" belong in the last. Bruce, Cobalt and Animikie might well have been used instead of Lower, Middle and Upper Huronian.

Both titles and text show the emphasis placed on formations as well as history. There are many columnar sections and structure diagrams, as well as maps of selected regions. Dr. Moore's extensive work in the West enables him to treat western geology in greater detail than is done by Schuchert and Dunbar. Life is discussed by eras and suberas rather than by periods, a method that the author considers confusing and philosophically unjustified. There is justice in his contention; even the paleontologist must grant that historical geology too often has been presented as a history of life with little more than a geologic background. This is most obvious, among recent books, in L. C. Snider's *Earth History*, reviewed in this journal last year. Paleozoic formations, history and life receive 280 pages, Mesozoic 123, and Cenozoic 124. There is a seven page bibliography of titles suited to the advanced student, whose knowledge may come from original papers.

Physically, the book is less pleasing than that of Schuchert and Dunbar; illus-

trations of fossils have been poorly printed. Some are insufficiently inked, while others lose through the paper, resembling that of other McGraw-Hill books in which halftones often are not clear.

Dr. Field's text is addressed to beginning students and stresses western North America. In a preface addressed to teachers, the author announces that his "interpretation of the existing conditions in the teaching of historical geology is that we are attempting to do too much in the time allowed, and that we are losing sight of the main problem, which is to try to help the student understand how the history of the earth has been deciphered . . . and thus afford [him] a better opportunity of testing for himself the geologist's interpretations. . ."

The book is built to meet these objections. Part I presents the history of stratigraphy, the nature and meaning of sedimentary rocks, and the technique of correlation. Part II describes such selected regions as the Grand Canyon, Niagara Falls, the Appalachian and Scotch highlands, Yellowstone Park and the Big Horn Basin. Chapters are admirably conceived; though marred by apparent haste of preparation, they emphasize the points that Field considers essential. They may point, therefore, to a new plan of teaching, which will do as well as the conventional one in preparing elementary students of geology proper, and a great deal more in bringing it to the thoughtful attention of those who expect to enter other fields—CARROLL LANE FENTON.

AN INTRODUCTION TO THE STUDY OF FOSSILS, by Hervey W. Shimer. Second edition. New York: The Macmillan Company, 1933. xviii + 496 pp. $4.00.

MAN AND THE VERTEBRATES, by Alfred Sherwood Romer. Chicago: University of Chicago Press, 1933 vii + 427 pp. $3.00.

Professor Shimer's is the one textbook of paleontology which combines the taxonomic and morphologic method with a consistent interpretation of fossils through the structure, physiology and ecology of related living forms. It thus meets the need of those teachers who do not, or cannot, require botany and zoology as preparation for paleontologic training.

The present edition presents no radical departure from that of 1914, but shows substantial improvement in detail. The morphologic discussions are modernized, taxonomic changes are incorporated or indicated, illustrations are better. The many question lists are consistent with the book's plan as an introduction to the subject—though one suspects that many of them will puzzle graduates of advanced taxonomic courses. By discussing important examples the text meets practical laboratory needs more effectively than does any other in English.

Romer's *Man and the Vertebrates* shares the conception of paleontology as a biologic subject, but is designed to supplement lectures. Its first 262 pages contain a simple yet comprehensive survey of vertebrate anatomy, taxonomy and environmental relationships, with good and abundant illustrations. These are followed by a chapter on human races, and 134 pages devoted to anatomy and embryology. It is obvious, then, that other vertebrates are included as a background for man, a procedure which reflects the viewpoint of most so-called survey courses. Philosophically, such a course is questionable; practically, it probably is an effective method of inducing students to think of organisms that they generally ignore. The volume is one of the best that has emerged from such courses, as well as a prolific source of collateral reading for others in zoology or geology—CARROLL LANE FENTON.

ENTOMOLOGY WITH SPECIAL REFERENCE TO ITS ECOLOGICAL ASPECTS. by Justus Watson Folsom, revised by R. A. Wardle. Philadelphia: P. Blakiston's Son & Co., 1934. ix + 605 pp., 5 pls., 308 figs. $4.00.

Among the many textbooks of entomology this revised edition will immediately find its place because of its novel character in laying emphasis on ecological aspects. In fact two-thirds of the volume is devoted to the latter and reveals many new and interesting facts and interpretations obtained from a thorough examination of recent literature. An appended bibliography of carefully selected titles arranged in accordance with the chapters will undoubtedly stimulate the consultation of original sources and thereby materially assist the student in his work. This book is strong evidence for the ever increasing public and scientific interest in all matters and problems pertaining to entomology. Because of its broad background and inclusive character it should be consulted with profit not only by the professional but also by the general biologist. —TH. JUST.

THE PRAIRIE, by J. E. Weaver and T. J. Fitzpatrick. Ecological Monographs, vol. 4, pp. 109-295, 1934.

There are few vegetational types in the United States that have been studied ecologically as thoroughly as the Prairie. This monograph is the third in a series devoted to the analysis and description of a vanishing vegetation and will therefore serve as a permanent document for future workers. Extensive field work over a period of years led to the recognition of several grassland types which are discussed in full. A large portion of the monograph deals with general aspects, such as climate, soil, the forbs and their ecological significance, seasonal aspects, growth, and succession. The complexity of composition of the Prairie is evident on the basis of this work which represents an outstanding example of investigation of American ecology. Both authors have known the Prairie for a long time and their observations prove their familiarity in every respect. It can only be hoped that by such painstaking and thorough studies other vegetational types will eventually become as well known as the Prairie.—TH. JUST.

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